Dr.M.H.M.G.N.H. Librar
581 HOW
5539
5539
581 HOW

581
How

1679

A SYSTEMATIC STUDY OF THE GENUS LESSINGIA CHAM.

BY

JOHN THOMAS HOWELL

Government of Karnataka
Dr. M. H. Marigowda National Horticulture Library
Directorate Of Horticulture Lalbagh,
Bangalore - 560 004

ACC. No. 5539

CALL No. 581 HOW

University of California Publications in Botany
Volume 16, No. 1, pp. 1–44, 70 figures in text
Issued August 5, 1929

University of California Press
Berkeley, California

Cambridge University Press
London, England

Acc No - 5539

581 HOW
5539

A SYSTEMATIC STUDY OF THE GENUS LESSINGIA CHAM.

BY

JOHN THOMAS HOWELL

INTRODUCTION

History

Lessingia germanorum Cham., the type species of the genus, was first collected by Adelbert von Chamisso in October, 1816, on the sand hills of the San Francisco peninsula (Chamisso, 1820). The genus *Lessingia* was first described in 1829 by Chamisso and was named in honor of the Lessings, a German family of scientists and authors. Twenty-nine species have been described to the present time, seven of which are retained as species in this work.

Relationships

Lessingia belongs to the Astereae or *Aster* tribe of the Compositae. Because of the absence of ray-flowers in the genus, Bentham (1873) placed *Lessingia* in the *Solidago* group or the subtribe Homochromeae, noting however its possible relationship to the *Aster* group or the Heterochromeae. Gray in the Synoptical Flora of North America and Hoffman in Die Natürlichen Pflanzenfamilien follow Bentham's arrangement. *Lessingia,* however, has its closest relative in the heterochromous genus *Corethrogyne.* Gray (1874) pointed out the closeness of *Lessingia* to *Corethrogyne* in a review of the former in the Botany of the United States Exploring Expedition. H. M. Hall (1907) in the Compositae of Southern California indicates this relationship also, saying, "*Lessingia* finds its nearest relative in *Corethrogyne,* which it closely resembles in habit and technical characters of the involucre, anther-tips, and style appendages."

Lessingia and *Corethrogyne* probably represent the differentiation of a single phylogenetic line derived from the *Aster* type. The two genera appear to be most closely related to section *Machaeranthera* of *Aster* which centers in the widely distributed and variable species, *Aster canescens* Pursh. Greene (1896) in his defense of

Machaeranthera Nees as a generic segregate of *Aster* writes: "While *Machaeranthera* as a genus does not in any way intergrade with *Aster*, it does present everywhere marks of a much closer affinity for two other allied genera, namely, *Corethrogyne* and *Lessingia*." *Corethrogyne* is closer to *Aster* than *Lessingia* because of its perennial habit and ligulate heads but differs from *Aster* in the more slender involucre, sterile ray-flowers, and comose style appendage. *Lessingia*, a highly unified and distinctive genus, differs from *Corethrogyne* in that it is a group of annual herbs with discoid heads and with the outer corollas of the head generally enlarged and palmate.

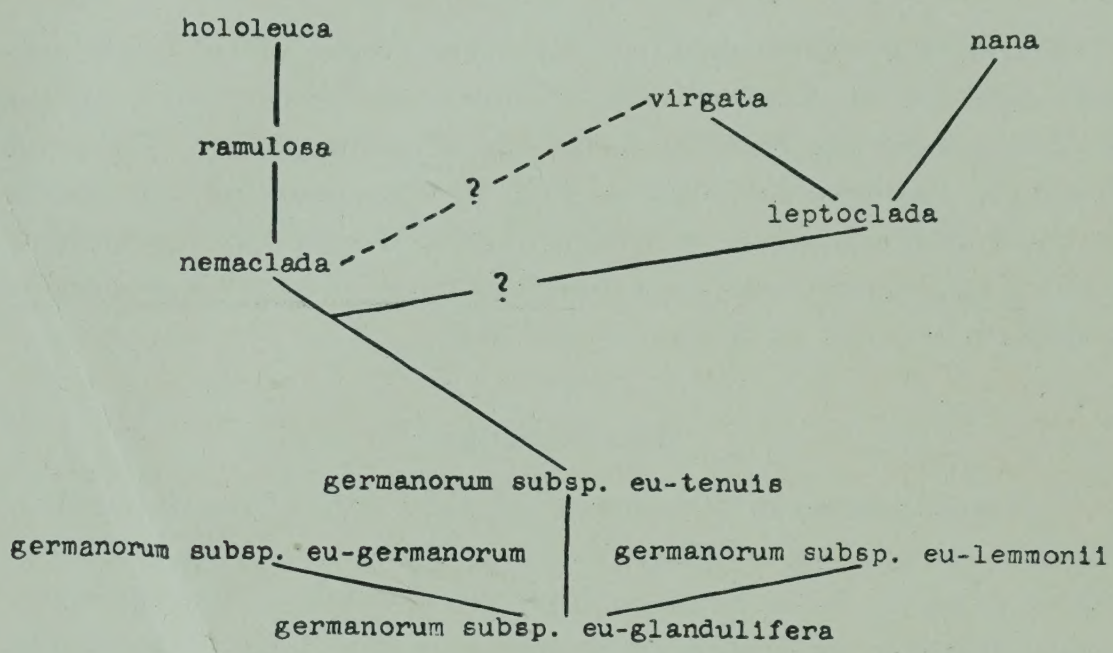


Fig. 1. Chart of probable relationships of species and subspecies of *Lessingia*.

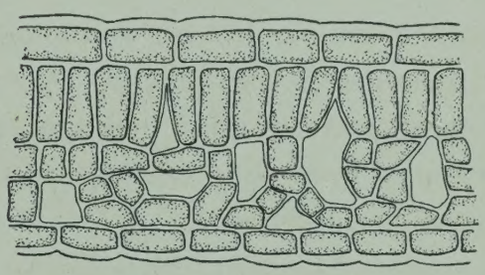
Relations within the genus (fig. 1) are difficult to trace because of its homogeneous character. *Lessingia germanorum* subspecies *eu-glandulifera* (*L. glandulifera* Gray) is taken as the oldest form from which the other species and subspecies are probably derived, directly or indirectly. In that subspecies the callous grain at the apex of the cotyledons, the absence of punctate glands, the yellow color of the flowers, the large number of flowers in each head, and the distinct pappus bristles are believed to be the primitive characters of the genus. After comparing the similarities and differences of structural characters in the several species, the lines of development appear to be as follows: from *L. germanorum* subspecies *eu-glandulifera* there are probably three lines of development, a first, terminated by *L. germanorum* subspecies *eu-lemmonii* (*L. lemmonii* Gray) characterized

by specialized style appendage; a second, by way of *L. germanorum* var. *pectinata* to *L. germanorum* subspecies *eu-germanorum* (*L. germanorum* Cham.), characterized by a reduction of glands and change of habit; a third, to *L. germanorum* subspecies *eu-tenuis* (*L. tenuis* Cov.) characterized by change of habit, instability of flower color, and tendency for the pappus bristles to unite. *Lessingia nemaclada* var. *albiflora* probably arises near *L. germanorum* subspecies *eu-tenuis* and it also has variable flower-color but is marked by different habit and by the presence of both punctate and stipitate glands. *Lessingia nemaclada* var. *mendocina,* characterized by subulate style appendages, is a well marked development from *L. nemaclada* var. *albiflora.* Typical *L. nemaclada,* a form very close to var. *mendocina,* is marked by its numerous slender branchlets, minute cauline leaves, and small narrow heads. It is believed that *L. nemaclada* var. *mendocina* by reduction of style appendage and disappearance of punctate glands passes to *L. ramulosa. Lessingia hololeuca* is closely related to *L. ramulosa* but differs from it in number of glands, shape of corolla, character of style appendage, and pappus. *Lessingia leptoclada* is probably in a line of development originating near *L. nemaclada* but differentiated from it by the character of the involucre and the absence of stipitate glands. *Lessingia nana* and *L. virgata* are believed to be well marked developments from *L. leptoclada.* The former is marked by habit, involucral bracts, and pappus, the latter is marked by habit, occasional stipitate glands, and variability in the length of the style appendage.

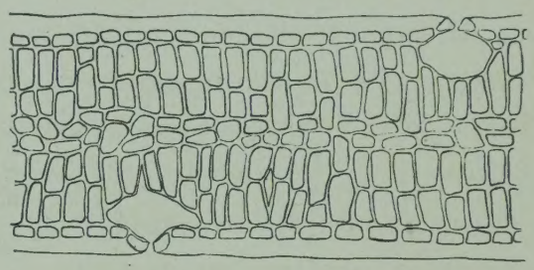
Ecology

Lessingia is a genus of annual herbaceous plants blooming in late spring, summer, and autumn. The species are among the semi-xerophytic plants which are characteristic of the dry, open plains and lower hills of California, blooming after the spring flora has passed. Some of the late annual herbs often associated with *Lessingia* are species of *Eriogonum* including *Eriogonum thurberi, E. gracile, E. virgatum, E. vimineum,* and *E. dasyanthemum, Eremocarpus setigerus, Epilobium minutum, Navarretia squarrosa, Trichostema lanceolatum, Trichostema laxum, Cordylanthus pilosus, Cordylanthus rigidus, Stephanomeria virgata, Centromadia pungens, Hemizonia virgata, Calycadenia multiglandulosa, Madia elegans,* and *Lagophylla ramosissima.*

During the vegetative period there are generally two marked developmental stages. The first persists through the early growth of the seedling to the end of the wet season, the second includes the later development and season of maturation. The first stage is marked by acaulescent or very low caulescent plants with mesophytic type of leaves, tomentose-pubescent or glabrate. In section these leaves are seen to be composed of large cells with numerous, large intercellular spaces, and the cutinized layer of the epidermis is relatively thin. About half the leaf is composed of spongy parenchyma and there is only one layer of the palisade parenchyma below the upper epidermis (fig. 2). Thus these leaves show tissues that are typical of the leaves



2



3

Figs. 2, 3. *L. ramulosa* var. *micradenia* J. T. Howell. 2, cross-section of leaf collected May 8, 1927, showing mesophytic character. J. T. Howell No. 2360. × 200; 3, cross-section of leaf collected September 17, 1925, showing xerophytic character. Mason No. 2233. × 200.

of mesophytes of meadow and forest. After the rainy season is over and the ground has been parched by the constant sun, the upright shoots of *Lessingia* develop. The basal leaves dry and the ultimate branchlets bear reduced, bract-like leaves, often intensely glandular, sometimes tomentose. These leaves are markedly xerophytic in character. The cutin is often as thick as or thicker than the lumen of the epidermal cells (figs. 3, 18, 45). Palisade cells constitute the dominant parenchymatous tissue of the leaf and form a single or double layer beneath both upper and lower epidermises. Small, closely packed, spongy parenchyma cells occupy a very limited space between the palisade layers (fig. 3). Thus in the life-cycle of a single individual can be found near-extreme types of ecological variation.

Distribution

Lessingia is found in that district termed by students of the distribution of the Compositae the Mexican region, an area including California and Central America as well as Mexico. In the northern

part of this area where the Compositae have developed so remarkably, *Lessingia* is found, extending from northern California south into northern Lower California and east into western Arizona. It is nearly a California endemic, *L. germanorum* subspecies *eu-glandulifera* and *eu-lemmonii* being the only forms which extend beyond the state.

In studying the distribution of the species of *Lessingia* an attempt has been made to determine the center of distribution of the genus. This center is believed to be in the rugged montane area at the southern end of the San Joaquin Valley where the southern Sierra Nevada joins the inner south Coast Ranges, an area which is here called the Tehachapi region. This region is believed to be the center of distribution for the following reasons:

1. It is near the center of distribution of the largest and most widely distributed species, *L. germanorum,* and within this region three of the four subspecies of that species occur. This is significant because in this work *L. germanorum* is believed to be the most primitive species as deduced from morphologic criteria.

2. In this region are found three species besides the primitive *L. germanorum.* In the Sierra Nevada region five species are found, but two of these, *L. nana* and *L. virgata,* are perhaps the most highly specialized in the genus and are considered closely related to *L. leptoclada.* However, this latter region cannot be considered the center of distribution of *L. germanorum,* an important consideration in favor of the Tehachapi region.

3. The Tehachapi region is a focus for what are believed to be the paths of dispersal for both the species of the genus and the subspecies of *L. germanorum:* one, south through southern California to Lower California; two, east to the Mohave Desert and Arizona; three, north through the Sierra Nevada foothills to Mount Shasta and thence south through the Coast Ranges to the San Francisco Bay region; four, north through the south Coast Ranges and San Joaquin Valley to the San Francisco Bay region.

Although the Tehachapi region is not the region where the greatest number of species occurs, a most important criterion in determining the center of distribution of a genus, it is believed that the other evidence distinctly indicates the Tehachapi region as the center of distribution. A study of the distribution of the species in the light of morphologic evidence and a similar consideration of the distribution of the subspecies and varieties of *L. germanorum* outline most definitely the paths of dispersal described above, and the focus of

these paths must be the center of distribution. And moreover, in a small genus like *Lessingia,* the characters and relationships of which seem to indicate a relatively recent origin and the distribution of which is confined to a definite and narrow field, it would appear that the utmost importance might be attached to the distribution of what is believed to be the most primitive species in determining the center of distribution of the genus.

The distribution of *Lessingia* in life-zones is fairly definite in most species, the center of zonal distribution being Upper Sonoran. Only two of the species are found in more than one life-zone. *Lessingia nemaclada, L. ramulosa, L. virgata, L. nana,* and *L. hololeuca* occur in a single life-zone, the Upper Sonoran. *Lessingia leptoclada* occurs in two zones, the Upper Sonoran and Transition zones. The widespread species, *L. germanorum,* is most abundant in the Lower and Upper Sonoran zones but it also occurs in the lower Transition zone in southern California.

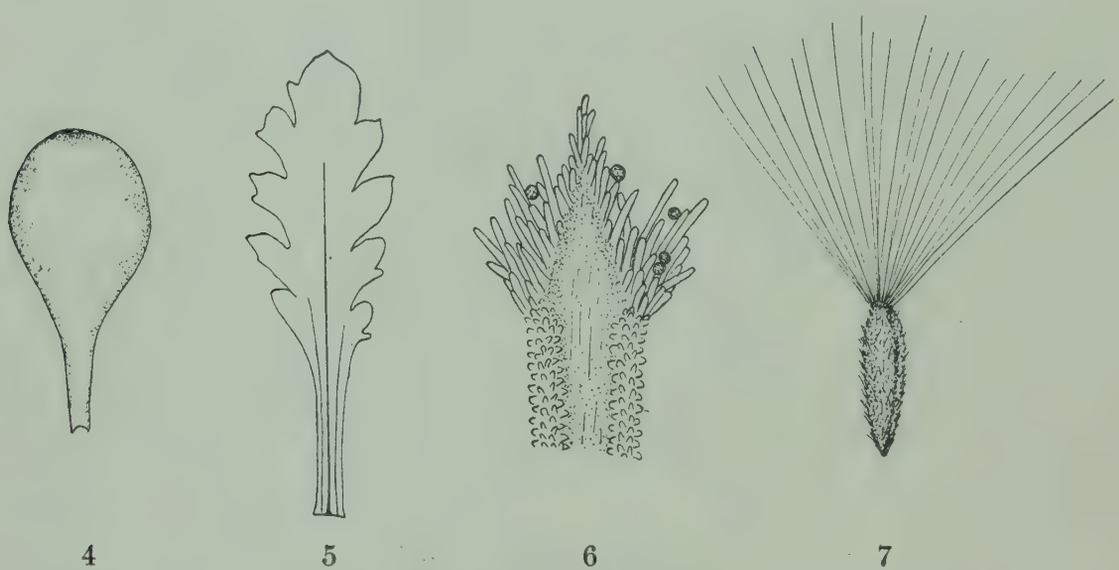
In considering the distribution of the species of *Lessingia* it is of interest to contrast the range of several species and varieties with the endemic areas recently named by Jepson (1925). The correspondence between the range of a species or a variety and the extent of an area outlined is frequently very striking and decided. In the Sierran region of the Low Foothill area, *L. nana* extends from Kern County to Eldorado County, and *L. virgata* ranges from San Joaquin County to Tehama County. *Lessingia ramulosa* is found in the Franciscan area north of San Francisco Bay while the distinct variety, *L. ramulosa* var. *adenophora,* is confined to the mountains of the Napa–Lake area. Almost coextensive with the Franciscan area is the range of *L. hololeuca;* the variety, *L. hololeuca* var. *arachnoidea,* is found in the same area south of San Francisco Bay. *Lessingia nemaclada* var. *mendocina* is nearly confined to the Tehaman area, and *L. germanorum* var. *ramulosissima* extends beyond the Mohavan area only north to Owens Valley. The well marked variety, *L. germanorum* var. *pectinata,* is found only on the coast sand hills of the Lucian area, and typical *L. germanorum* is restricted to the same type of habitat on the San Francisco peninsula in the Franciscan area.

Field Work and Garden Cultures

In connection with the revision of the genus *Lessingia* extensive field work was done. In the field it has been possible to observe the plants under natural conditions and also to observe how characters vary when the environment changes. Even under uniform conditions the plants in a small area have been found to vary considerably, depending upon the robustness of the individuals. For example, young plants of *L. germanorum* var. *ramulosissima* with shallow roots bloom while the herbage is still white-tomentose, and robust plants with deep tap roots do not bloom until an intricately branched plant, characterized by green, glandular herbage, has grown. The differences in this instance were so great that the young plant was considered another variety until the two forms were seen and collected in the field (cf. J. T. Howell Nos. 2493, 2673). It has been found also that one species often presents several different aspects as it develops from youth to maturity. In several instances it has been possible to show that a young individual has received one specific name and a matured specimen of the species has been given another specific name. The type of *L. hololeuca* Greene is not a mature plant and the isotypes of *L. imbricata* Greene and *L. bakeri* Greene that have been examined are matured plants of *L. hololeuca.* In the field and in the garden cultures it has been possible to follow such changes in appearance. The type localities of several species were visited and the characters of the topotypes collected have been of assistance in determining the specificity of the plants concerned. The topotypes of *L. germanorum* showed it to be but a modified and highly localized form of a large and variable species. Specimens from the type locality of *L. bicolor* Greene compared most favorably with the type specimens of *L. ramulosa* Gray so that there is no doubt that the two are the same species.

Supplementing the study of *Lessingia* in the field and in the herbarium, five species, two subspecies, and several varieties were grown in culture at the Botanical Garden of the University of California in the Berkeley hills, *L. nana, L. virgata,* and *L. germanorum* subspecies *eu-lemmonii* being the only major forms not grown. From the cultures, valuable data on the life-histories and seedling habits were obtained, the most important results being summarized in the following outline.

In the three subspecies of *L. germanorum* that were grown, *eu-germanorum, eu-glandulifera,* and *eu-tenuis,* the cotyledons were marked with a conspicuous callous grain at the apex (figs. 4, 11). This was lacking from the cotyledons in all other species of the genus that were cultivated (figs. 32, 34, 48, 61). *Lessingia leptoclada* and *L. hololeuca* before this have frequently been confused, for these two species exhibit a striking resemblance in floral structures and parallelism in variation which make them seem more closely related than they actually are. The rugulose-veined cotyledons of *L. leptoclada* together with its more diminutive seedling habit (figs. 34, 35) at once



4 5 6 7

Figs. 4–7. *L. germanorum* Cham. 4, cotyledon, from garden cultures. × 5; 5, basal leaf, from garden cultures. × 1; 6, appendage of style-branch. J. T. Howell No. 2180. × 60; 7, achene and pappus. J. T. Howell No. 2180. × 7½.

showed that species to be specifically distinct from *L. hololeuca* which has a robust seedling habit and smooth cotyledons (figs. 61, 62). It is believed that the great similarity shown in the developmental stages of *L. hololeuca* and *L. ramulosa* indicates a close relationship between the two species, a relationship to be expected from a study of their distribution. In culture the habits of nearly all the mature plants were markedly more robust than plants of the same species or variety in natural habitat, and forms that are characterized by simple stem were diffusely branched from the base. This change of habit and increase of vigor are believed to be due almost entirely to cultivation and to lack of competition of other plants. Probably owing to the cooler climate of the San Francisco Bay region, *L. germanorum* var. *vallicola* and *L. germanorum* var. *glandulifera* were lower in habit than plants of these varieties growing under natural conditions, and

in the case of the latter variety, native of the hot interior valleys of southern California, few flowers and no fruit were produced. The herbage of these varieties, however, was typically glandular. Plants of *L. germanorum* preserved the spreading, decumbent habit characteristic of the plants growing on the foggy seaward side of the San Francisco peninsula and no development of glands on the leaves was induced by the warmer, drier climate of the Berkeley hills. Herbarium specimens of the seedlings in different stages, as well as specimens of the matured plants, were prepared from time to time as a permanent record of the developmental stages. These specimens are in the author's collection and are not cited in this work.

Acknowledgments

The revision of the genus *Lessingia* was undertaken at the suggestion of Professor W. L. Jepson of the University of California. For his constant interest and assistance in the work the author is very grateful. The author also greatly appreciates the privileges extended to him by the officers and owners of the various herbaria in which the *Lessingia* material is deposited. The abbreviations used to indicate the sources of material are:

University of California, (UC)
Dudley Herbarium, Stanford University, (S)
California Academy of Sciences, San Francisco, (CA)
Pomona College, Claremont, (Cl)
W. L. Jepson, (J)
F. W. Peirson, (P)
H. L. Mason, (M)
J. T. Howell, (H)

Types of several species were kindly loaned by the officers of the Gray Herbarium (G) and the United States National Herbarium (US). To several of his friends, the author is grateful for valued gifts of *Lessingia* material which proved to be helpful in the work of revision.

TAXONOMIC TREATMENT

Lessingia Chamisso, Linnaea, 4:203, 1829; DeCandolle, Prodromus, 5:351, 1836; Bentham and Hooker, Genera Plantarum 2, pt. 1:257, 1873; Gray *in* Brewer and Watson, Botany of California, 1:306; Gray, Synoptical Flora 1, pt. 2:161, 1884; Hoffman *in* Engler and Prantl, Die Natürlichen Pflanzenfamilien 4, heft 5:152, 1890; Greene, Flora Franciscana, 375, 1897; Jepson, Flora of Western Middle California, 561, 1901; Hall, Compositae of Southern California, Univ. Calif. Publ. Bot., 3:66, 1907; Jepson, Manual of the Flowering Plants of California, 1040, 1925.

Erect or depressed annual herbs of summer and autumn. Herbage (leaves and stems) tomentose or glabrate, generally glandular, the glands punctate-sessile or stipitate. Leaves alternate, sessile, entire, serrate, or deeply lobed, 3-nerved; basal leaves rosulate, numerous, with slender petiole-like base; cauline leaves becoming sessile by a broad, often slightly decurrent base and passing into the upper reduced, scale-like leaves. Inflorescence glomerate, paniculate or spicate, the heads small, 3–38-flowered. Involucres narrowly turbinate to narrowly campanulate, 0.4–1.2 cm. high, the bracts numerous in many series, loose or imbricate, the tips often glandular-herbaceous, appressed or squarrose to recurved. Receptacle slightly convex, areolate-pitted. Flowers perfect. Corollas yellow, lavender, rose, or white, discoid, with a line of inward pointing hair-like processes on the nerve below each sinus; outer corollas enlarged and generally palmate-reflexed, lobes 5; inner corollas tubular to funnel-form, inner sinus more deeply cleft. Anthers cordate, without basal appendage, the apical tip subulate-pointed; pollen echinulate, 0.02 mm. in diameter. Style-branches becoming exserted, flattened, 0.5–2.5 mm. long,[1] the appendage 0.14–1 mm. long, a penicillate tuft, truncate with or without a cusp, or becoming subulate. Achenes turbinate, white-silky with upwardly appressed hairs, round and turgid or compressed, pericarp mottled with brown and black; pappus tan to dark brown or red, the bristles in one or two series, unequal, distinct or becoming united into sets bristly at the end, sometimes reduced to 5 simple, paleaceous awns; cotyledons spatulate, with or without a callous grain at apex.

KEY TO THE SPECIES

Glands spheroidal, short-stipitate; corollas yellow, sometimes with a purplish band in the throat (corolla sometimes white or pinkish in var. *tenuis* of No. 1) ..... 1. *L. germanorum.*

Glands punctate, tack-shaped, or none; corollas white to lavender or rose color, never yellow.

Cauline leaves with punctate glands.

---

[1] The lengths of style-branches given throughout this work do not include the length of the appendages of the style-branches.

Plants of erect habit; tips of inner involucral bracts herbaceous or scarious; pappus bristles 40 or less, light to dark brown.
Inflorescence cymose-paniculate.
Cauline leaves with two kinds of glands, punctate and stipitate ..... 2. *L. nemaclada.*
Cauline leaves with punctate glands only ..... 3. *L. leptoclada.*
Inflorescence spicate, virgate (glomerate in var. *glomerata* of No. 4) ..... 4. *L. virgata.*
Plants of depressed and dwarf habit; tips of the inner involucral bracts white, crustaceous; pappus bristles 50–70, dark brown or bright red ..... 5. *L. nana.*
Cauline leaves without punctate glands.
Cauline leaves with tack-shaped glands; outer corollas only slightly enlarged, not palmately spreading ..... 6. *L. ramulosa.*
Cauline leaves not glandular; outer corollas conspicuously enlarged, palmately lobed, and spreading ..... 7. *L. hololeuca.*

When all the species have been grown as cultures it will probably be found that the cotyledons of the yellow-flowered species are marked with a conspicuous callous grain at the apex, and that the callous grain is entirely lacking in the lavender-flowered species. This distinction is true for all species that have been grown, the only species not observed being *L. virgata, L. nana,* and subspecies *eu-lemmonii* of *L. germanorum.*

1. **Lessingia germanorum** Chamisso, Linnaea, 4: 203, 1829

Figures 4–7

Plants branching widely from near the base, decumbent or seldom strictly erect, 15–30 cm. high; herbage and young stems gray-green with matted tomentum; glands few on the involucral bracts, the glandular excretion not odorous or bitter to taste; basal leaves numerous, slender-oblanceolate to oblong, up to 3 cm. long, mucronulate, pinnately cleft into four or five pairs of oblong to lanceolate, acute or abruptly acute lobes; cauline leaves 0.5–1.5 cm. long, oblong-oblanceolate, broadly sessile or with a broad petiole-like base, pinnatifid, acute, the uppermost leaves small, linear to oblong-obovate, saliently toothed to subentire; heads single, 25–38-flowered; involucre narrowly campanulate, 5–7 mm. high, the involucral bracts numerous in many series, loosely imbricated, the tips recurved; corollas deep lemon-yellow often with a brownish band in the throat, the outer corollas palmate, the inner corollas funnel-form to tubular; style-branches 0.9–1.3 mm. long, appendage 0.3–0.38 mm. long with or without a short cusp; achene 1.5–2 mm. long, long-turbinate; pappus bristles 21–31, in one series, generally free or sometimes with 2–4 united at the base, 2–4 mm. long; apex of cotyledon very obtuse and with conspicuous callous grain.

Near the ocean on the dune hills of the San Francisco peninsula in San Mateo and San Francisco counties, 100 to 300 ft. Aug.–Nov.

Localities.—Marine Hospital, Presidio, San Francisco, T. S. Brandegee, July, 1890 (UC); Mountain View Lake, San Francisco, Jepson, Oct., 1894 (J); Lone Mountain, San Francisco, J. T. Howell Nos. 2180, 2288 (seedlings, H); Lake Merced, San Francisco, Eastwood, Aug. 7, 1913 (CA); Lake Merced, San Francisco, J. T. Howell No. 2233 (H).

The specimens from the vicinity of the San Francisco Presidio may be considered topotypes of this, the first described species of *Lessingia.* In his journal Chamisso (1820) writes, "The presidio and mission of San Francisco lie on this tongue of land (i.e., the San Francisco peninsula), which, with its hills and downs, was the narrow field which lay immediately open to our researches." It is interesting that in the present work plants typical of the species are found to be confined to the "narrow field" explored by Chamisso.

The treatment of this complex and variable species, taken in its broadest sense, differs somewhat from that of the other species in this work. In keeping with the interpretation of the other species of *Lessingia* it has not been possible to recognize *L. glandulifera* Gray, *L. lemmonii* Gray, and *L. tenuis* (Gray) Cov. as species distinct from *L. germanorum* Cham. As indicated in the introduction, *L. germanorum* subspecies *eu-glandulifera* is believed to be the center of variation in the species *L. germanorum* as it is considered here. Since typical *L. germanorum* Cham. is a highly specialized and localized form, the probable relationships within the species as a whole are discussed in reference to *L. germanorum* subspecies *eu-glandulifera.*

Lessingia germanorum Cham. (*L. germanorum* subspecies *eu-germanorum*) in typical form is characterized by spreading habit, by persistent tomentum, and by almost complete absence of glands. The few glands are confined to the involucral bracts and the glandular secretion is neither bitter nor odorous. *Lessingia germanorum* Cham. is very closely related to *L. germanorum* subspecies *eu-glandulifera* by *L. germanorum* var. *pectinata,* but in this variety the habit is generally suberect, the upper leaves are glabrate-glandular, and the secretion of the numerous glands is bitter and odorous.

Lessingia lemmonii Gray is characterized by a subulate style appendage varying from 0.7 to 1 mm. long. This character is approached in *L. germanorum* subspecies *eu-glandulifera,* making *L. lemmonii* as a species untenable. The following data, taken from sheets in the herbaria indicated, show how variable is the length of the style appendage in varieties of *L. germanorum* subspecies *eu-glandulifera* and how nearly it approaches the length of the appendage in *L. lemmonii* Gray:

Lessingia germanorum var. *tenuipes:*
Templeton, J. T. Howell No. 3005 (H) ..... 0.17 mm.
Orcutt, J. T. Howell No. 2998 (H) ..... 0.2 mm.
Lessingia germanorum var. *vallicola:*
Parkfield, Hall No. 12239 (H) ..... 0.19–0.22 mm.
Manteca, J. T. Howell No. 3065 (H) ..... 0.22 mm.
Three Rivers, J. T. Howell No. 3068 (H) ..... 0.25 mm.
Lessingia germanorum var. *pectinata:*
Del Monte, K. Brandegee, July, 1910 (UC) ..... 0.2 mm.
Near Del Monte, Peirson No. 5300 (H) ..... 0.26 mm.
Morro sands, Eastwood No. 14961 (H) ..... 0.3 mm.
Lessingia germanorum var. *glandulifera:*
Pasadena, G. B. Grant (UC) ..... 0.3 mm.
Pine Valley, J. T. Howell No. 2981 (H) ..... 0.34 mm.
Claremont, Baker No. 3444 (CA) ..... 0.34 mm.
Warner's Hot Springs, A. Buttle (CA) ..... 0.39 mm.
Upland, Keck No. 259 (H) ..... 0.4 mm.
San Bernardino, Parish No. 3807 (CA) ..... 0.4 mm.
Mt. San Jacinto, J. T. Howell No. 2929 (H) ..... 0.4–0.46 mm.
Laguna Mountains, MacGregor No. 20 (S) ..... 0.54 mm.
Mt. San Jacinto, Hall No. 2626 (UC) ..... 0.5–0.6 mm.
Mt. San Jacinto, J. T. Howell No. 2909 (H) ..... 0.6 mm.
Mt. San Jacinto, W. Swarth (CA) ..... 0.6–0.68 mm.
Newhall, J. T. Howell, No. 3089 (H) ..... 0.6–0.65 mm.

Lessingia tenuis Cov. is characterized mainly by habit and appearance, all the morphological characters being found in forms of *L. germanorum* subspecies *eu-glandulifera*. *Lessingia tenuis* Cov. is generally branched from the base, the branches being flexuous and spreading. The leaves and branches are gray-green with persistent, somewhat appressed tomentum. Glands, which are few, are found only on branchlets, uppermost leaves, and involucral bracts. Two variants have been described, the one occurring in the Mount Pinos region (*L. tenuis* [Gray] Cov., figs. 8–10), the other ranging from San Luis Obispo County north to Santa Clara County (*L. parvula* Greene, figs. 11–14).

The two forms differ chiefly in the yellow-colored corollas and the pinnate-lobed leaves of the northern plants, and the varicolored corollas and entire or subentire leaves of the southern plants. If the northern form did not exist, the plant of the Mount Pinos region would be an excellent species, but as the facts are, the form called *L. tenuis* intergrades as completely with *L. parvula* as the latter intergrades with forms of *L. germanorum* subspecies *eu-glandulifera*. In July, 1926, the author collected a series of plants in the Mount Hamilton region in San Antonio Valley, Santa Clara County (J. T. Howell No. 2061) which grew on a uniform hillside in an area of less

than an acre in extent. In this collection a sequence can be arranged passing from plants which are tomentose and somewhat glandular to plants which are darkish green, without tomentum, and intensely glandular. The tomentose plants at one extreme of this collection are typical of *L. parvula* Greene, the green and glandular plants of the other extreme cannot be distinguished from *L. germanorum* subspecies *eu-glandulifera*. In this last form even the distinguishing characters of habit and appearance of the *tenuis–parvula* group are wanting. Other plants from the Mount Hamilton region which certainly are *L. parvula* Greene were collected by A. D. E. Elmer in San Antonio Valley in May, 1903, and in the same region at Isabel Creek, Mount Hamilton, by F. Murray Scott in May, 1923. The further growth of the plants from May until July apparently develops the characteristics of the subspecies *eu-glandulifera* shown in plants of the author's collection. For the above reasons *L. tenuis* Cov. (including *L. parvula* Greene) is believed to be definitely related to *L. germanorum* Cham. (*sens lat.*) and to be an integral part of that species.

In order to show more clearly and properly the relations which exist in *L. germanorum* as described here, it has been considered best to interpret the three well marked forms discussed above as subspecies, the remainder of the species about which the variation appears to center being a fourth and coequal subspecies.[2] Some will probably wish to interpret the four subspecies as four species and this can be done easily with only the necessary change of names, for the relation of the four, whether considered as species or subspecies, will be as explained above or as shown in the following key. The varieties described and named in this species are based on characters of nearly equal importance and are equivalent to varieties found under other species in this work.

---

[2] It is here proposed that the subspecific names in this paper be omitted when the name of a *Lessingia* of the *germanorum* complex is written, just as sectional and subgeneric names of genera are omitted when a species is named which occurs in such a section or subgenus. This procedure is making exception to the International Rules of Nomenclature which provide for quadronomial nomenclature but the procedure is not without precedent; for example, *Phacelia magellanica* (Lam.) Cov. subspecies *barbata* Brand forma *griseophylla* Brand (Das Pflanzenreich IV, 251:98, 1913) is given by MacBride as "*P. magellanica* (Lam.) Cov., f. *griseophylla* Brand" (Contrib. Gray Herb., n.s., 49:35, 1917), and is given by Jepson as "*P. magellanica* f. *griseophylla* Brand" (Man. Fl. Pl. Calif., 819, 1925). It seems to the author that this simple treatment of grouping varieties of a complex species into subspecies for elucidating relationships and simplifying discussions is very desirable and he has employed it in this paper because of its great convenience. But since he does not wish to introduce quadronomial nomenclature the subspecies are merely named and defined in the following key and are not further treated taxonomically.

KEY TO L. GERMANORUM AND VARIETIES

Glands very few, confined to the involucral bracts, the glandular secretion not odorous or bitter; sand hills near the ocean, San Francisco peninsula. (Subspecies *eu-germanorum* n. name.) ..... *L. germanorum.*

Glands generally numerous on branchlets, cauline leaves, and involucral bracts, the glandular secretion often odorous and bitter; south of San Francisco Bay to Lower California and east to Arizona.

Style appendage 0.14–0.7 mm. long; central and southern California west of the main mountain crest (except var. *tomentosa*).

Plants generally maturing at the close of the rainy season, the leaves rarely becoming xerophytic and glandular; style appendage 0.14–0.2 mm. long. (Subspecies *eu-tenuis* n. name.)

Basal leaves entire or very rarely few-toothed; corollas white, yellow, or rose color; Mt. Pinos region ..... *a.* var. *tenuis.*

Basal leaves toothed to pinnately divided; corollas yellow; Coast Ranges from San Luis Obispo County north to Santa Clara County ..... *b.* var. *parvula.*

Plants maturing in or after the middle of summer, the leaves generally markedly xerophytic and glandular. (Subspecies *eu-glandulifera* n. name.)

Style appendage 0.2–0.3 mm. long, truncate or rarely with a short cusp; San Joaquin Valley and bordering Sierra Nevada foothills south to Kern and Santa Barbara counties, west to the coast.

Plants spreading or less commonly erect; leaves pectinate-pinnatifid; coastal sand hills, Monterey and San Luis Obispo counties ..... *c.* var. *pectinata.*

Plants erect; leaves entire or pinnately lobed, or the lower divided; dry interior hills and valleys.

Cauline leaves more or less tomentose, the margins glabrate and glandular; basal leaves pinnately lobed; heads at end of short, leafy-bracted branchlets; San Joaquin Valley and bordering foothills, west in the south Coast Ranges to the Salinas Valley ..... *d.* var. *vallicola.*

Cauline leaves generally becoming glabrate and glandular; basal leaves divided into linear or lanceolate lobes and these often again toothed or lobed; heads at ends of elongated, slender branchlets; hills and valleys, Santa Barbara County north to Santa Clara County ..... *e.* var. *tenuipes.*

Style appendage 0.3–0.7 mm. long, acute to slender-subulate; southern California to Lower California.

Plants erect, 1–5 dm. tall, paniculately branched; cauline leaves generally glabrate, more or less glandular ..... *f.* var. *glandulifera.*

Plants low and compact, 10–12 cm. tall; leaves densely white-tomentose, glandular only along the margins; western Colorado Desert in San Diego County ..... *g.* var. *tomentosa.*

Style appendage 0.7–1.0 mm. long; Santa Barbara and Ventura counties to the Mohave Desert and bordering mountains; Arizona. (Subspecies *eu-lemmonii* n. name.)

Mature plants with leaves and stems above the base glabrate and glandular.

Plants intricately much-branched or young plants with few branches; glands numerous and conspicuous; involucres 4 mm. high; pappus 1–2 mm. long; Mohave Desert north to Owens Valley.....*h.* var. *ramulosissima.*

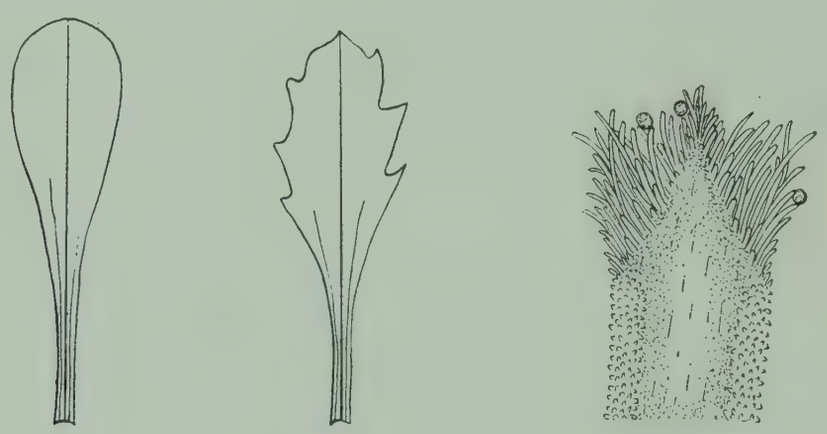
Plants much-branched but not intricately so; glands not numerous or conspicuous; involucres 5–6 mm. high; pappus 2–3 mm. long; north central Arizona; San Bernardino, Ventura, and Santa Barbara counties, California.....*i.* var. *lemmonii.*

Mature plants with herbage tomentose even to outer involucral bracts; glands on margins of upper leaves and involucral bracts; western Mohave Desert and bordering mountains in Kern, Ventura, and Los Angeles counties.....*j.* var. *peirsonii.*

a. **Lessingia germanorum** var. **tenuis** (Gray) J. T. Howell n. comb.

Figures 8–10

Lessingia ramulosa var. *tenuis* Gray, Bot. Calif., 1:307, 1876. *L. tenuis* Cov., Contrib. U. S. Nat. Herb., 4:124, 1893. *L. heterochroma* Hall, Univ. Calif. Publ. Bot., 3:67, 1907.



8 9 10

Figs. 8–10. *L. germanorum* var. *tenuis* J. T. Howell. 8, 9, basal leaves. J. T. Howell No. 3859. × 2. 10, appendage of style-branch, from type sheet, G. × 100.

Plants suberect or diffusely divided from the base, the branches flexuous, 3–12 (or 20) cm. long; basal leaves spatulate, 1–3.5 cm. long, 0.4–0.8 cm. wide, whitish-tomentose, becoming somewhat glabrate, margin entire or rarely serrate; upper leaves smaller and even scale-like, oblong to orbicular, lobed or entire, woolly-tomentose, the uppermost becoming viscidulose-pubescent or stipitate-glandular; the lower involucral bracts herbaceous and sometimes tomentose, the upper often glandular and purplish; flower color variable, white, yellow, rose color, or in a single head the outer flowers rose color and the inner yellow; style-branch 0.56–0.7 mm. long, appendage 0.14–0.2 mm. long, with no cusp; achene sometimes compressed, 2.5 mm. long; pappus bristles 15–25, mostly free to the base.

Dry open slopes in the Mt. Pinos region of Kern and Ventura counties, 4000 to 6000 ft. May–Aug.

Localities.—Head of Piru Creek (spelled Peru Creek on label), Ventura Co., Rothrock, Aug., 1875 (type of *L. ramulosa* var. *tenuis*, G); Frazier Mt., Ventura Co., Coville and Funston No. 1199 (G, S); Lockwood Valley, Ventura Co., Hall No. 6440 (type of *L. heterochroma* Hall, UC, S); Seymour Creek, Mt. Pinos, Ventura Co., Peirson No. 3242 (P, S, Cl, H); near Cuddy's Ranch, Mt. Pinos region, south Kern Co., J. T. Howell No. 3859 (flowers white, the inner becoming yellow, the outer becoming pinkish; H).

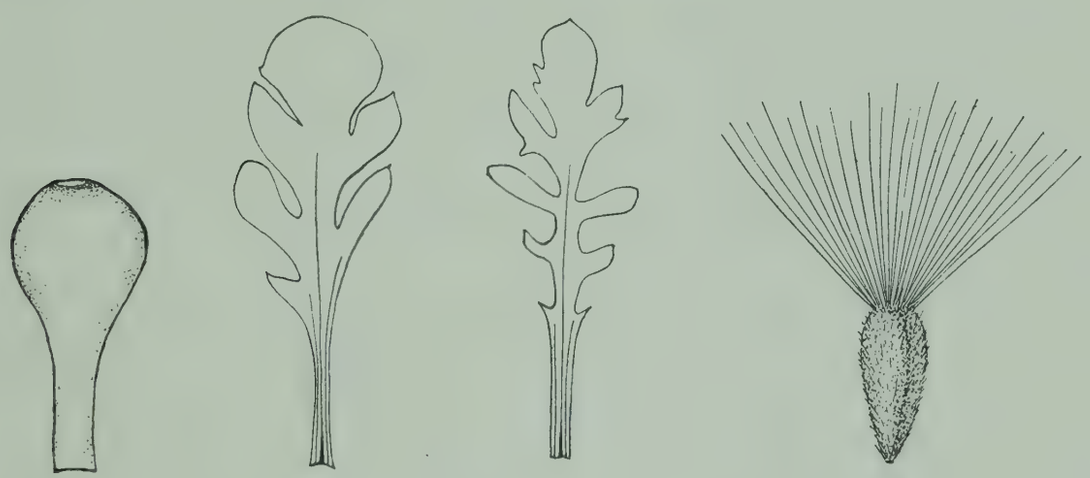
Lessingia heterochroma was described by Hall following extensive field studies in the Mount Pinos region. When this species was described it was not known that *L. ramulosa* var. *tenuis* Gray had the variable flower color that was believed to characterize the new species.

The type locality of *L. ramulosa* var. *tenuis* Gray is in the dry mountains of Ventura County, at the head of Piru Creek, at an elevation of 5100 feet.

b. **Lessingia germanorum** var. **parvula** (Greene) J. T. Howell n. comb.

Figures 11–14

Lessingia parvula Greene, Fl. Fran., 376, 1897. *L. tenuis* var. *jaredii* Jepson, Man. Fl. Pl. Calif., 1041, 1925.



Figs. 11–14. *L. germanorum* var. *parvula* J. T. Howell. 11, cotyledon, from garden cultures. × 10; 12, 13, basal leaves. J. T. Howell No. 2061. × 1½; 14, achene and pappus. J. T. Howell No. 2061. × 7½.

Similar in habit and tomentum to var. *tenuis;* basal leaves 2–3 cm. long, deeply and irregularly pinnately divided, the divisions entire or with one or two teeth; cauline leaves with salient acute lobes or entire; corollas yellow, generally with purplish ring in throat, the purplish color sometimes suffused along the lobes of the outer corollas; pappus bristles free to the base or several united at the base, rarely reduced to 5–8 paleaceous awns; cotyledons spatulate, 3–4 mm. long, apex obtuse, callous-grained.

Dry Coast Ranges from San Luis Obispo Co. north to Santa Clara Co., 1000 to 3000 ft. May–Aug.

Localities.—Vancouver Pinnacles, San Benito Co., Hall No. 9962 (UC); Hernandez, San Benito Co., Lathrop, Aug. 20, 1902 (like the more glandular forms of J. T. Howell No. 2061, S); San Antonio Valley, Santa Clara Co., Elmer No. 4350 (UC, S, CA, Cl); San Antonio Valley, Santa Clara Co., J. T. Howell No. 2061 (H); Isabel Creek, Mt. Hamilton, Santa Clara Co., Scott, May 20, 1923 (S, Cl); Stevens Creek Road, Santa Clara Co., Randall No. 89 (S). Two specimens having paleaceous pappus are: Estrella, San Luis Obispo Co., L. Jared (type of *L. tenuis* var. *jaredii* Jepson, UC); Santa Lucia Mts., K. Brandegee, June 10, 1909 (UC, S, Cl).

The type locality of *L. parvula* Greene is "in the interior of Monterey and San Luis Obispo Counties, Hickman, Lemmon."

Lessingia tenuis var. *jaredii* Jepson is characterized by a pappus reduced to 5 to 8 paleaceous awns. Throughout this work the tendency for pappus bristles to unite is not given varietal value but is considered a character variation within the species or variety where it occurs. This view is held because all but one species in the genus is known to show the tendency for the union of pappus bristles. Furthermore, the character is generally little more than a tendency, for in a well marked species or variety the variation often ranges from distinct bristles to paleaceous awns, this range sometimes occurring on a single plant.

c. **Lessingia germanorum** var. **pectinata** (Greene) J. T. Howell n. comb.

Lessingia pectinata Greene, Proc. Phila. Acad. Sci., 47:548, 1895. *L. glandulifera* var. *pectinata* (Greene) Jepson, Man. Fl. Pl. Calif., 1041, 1925.

Plants erect or spreading, branching from near the base; herbage sparingly glandular, the glandular secretion bitter; basal and cauline leaves pectinate-pinnatifid, the segments cuspidate; style appendage 0.2–0.3 mm. long, with or without a cusp; pappus bristles distinct, 34–48.

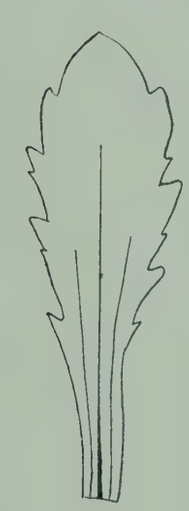
Near the coast in Monterey and San Luis Obispo counties. June–Sept.

Localities.—Near Monterey, K. Brandegee, June 16, 1908 (UC); three miles east of Monterey, Peirson No. 5300 (P, H); sand hills four miles east of Monterey, J. T. Howell No. 3020 (H); Pacific Grove, Jepson, Aug. 8, 1896 (J); Morro sands, San Luis Obispo Co., Eastwood No. 14961 (CA, Cl, H); San Luis Obispo district, Palmer, June, 1876 (UC).

Lessingia pectinata Greene was first described from specimens from the vicinity of Monterey.

d. **Lessingia germanorum** var. **vallicola** J. T. Howell n. var.

Figures 15–19



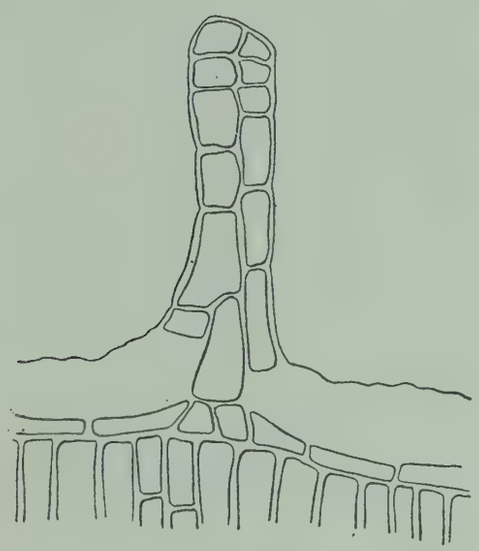
15



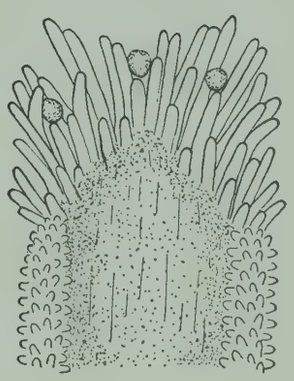
16



17



18



19

Figs. 15–19. *L. germanorum* var. *vallicola* J. T. Howell. 15, 16, basal leaves, from garden cultures. × 1; 17, cauline leaf. J. T. Howell No. 2011. × 1½; 18, glandular hair. J. T. Howell No. 2011. × 75; 19, appendage of style-branch. J. T. Howell No. 2011. × 100.

Plants 1–7 dm. tall, much-branched above; basal leaves oblanceolate, 1–6 (or 10) cm. long, pinnately lobed, tomentose; cauline leaves oblong to oblanceolate, pinnately lobed to saliently toothed, appressed-tomentose, the uppermost leaves ovate, entire or toothed, the margins glabrate and glandular or sometimes the whole leaf glandular; corolla yellow with purple band in the throat; style-branch 0.7–1 mm. long, appendage 0.2–0.25 mm. long without a definite cusp; pappus light tan to brown, the bristles distinct.

San Joaquin Valley and bordering foothills from Kern Co. north to the confluence of the Sacramento and San Joaquin rivers, west to the Salinas Valley, 50 to 3000 ft. June–Oct.

Localities.—Three miles west of Manteca on the valley highway, San Joaquin Co., J. T. Howell No. 3065 (type, H); San Miguel, San Luis Obispo Co., K. Brandegee, Oct. 12, 1912 (stocky from injury, UC); two miles south of Soledad, Monterey Co., Keck No. 464 (UC, Cl, H); Parkfield, Monterey Co., Hall No. 12239 (UC, H); Bakersfield, Kern Co., Davy No. 2393 (UC); Three Rivers, Tulare Co., J. T. Howell No. 3068 (H); Ahwahnee, Madera Co., G. B. Grant No. 4334 (UC); Minturn, Madera Co., Keck No. 489 (UC, Cl, H); Hopeton, Merced Co., J. T. Howell Nos. 1071, 2270 (seedlings, H); Merced River bridge one mile west of Livingston, Merced Co., J. T. Howell No. 3067 (H); Knight's Ferry, Stanislaus Co., J. T. Howell No. 2011 (H); Lathrop, San Joaquin Co., K. Brandegee, Sept., 1907 (UC); Antioch, Contra Costa Co., K. Brandegee in 1883 (UC, S).

This variety is the most robust in habit of all the forms of *L. germanorum* although some forms of the species in southern California become almost as tall and very much branched. The robust habit, the glabrate-glandular margins of the cauline leaves, and the uniformly short, blunt, style appendages mark this variety as it occurs in its typical form on sandy flats and opens of the San Joaquin Valley and bounding foothills. Some plants in this region have the uppermost leaves and involucral bracts glabrate-glandular, but more often tomentum is found even on the exposed parts of the involucral bracts. In the Salinas Valley a form is found which has all the upper leaves glandular and without tomentose hairs, a character in which it approaches var. *tenuipes* which is common in the region. However this plant is believed to be more closely related to var. *vallicola* than to var. *tenuipes* because of its habit and the numerous, short, leafy-bracted flowering branchlets.

e. **Lessingia germanorum** var. **tenuipes** J. T. Howell n. var.

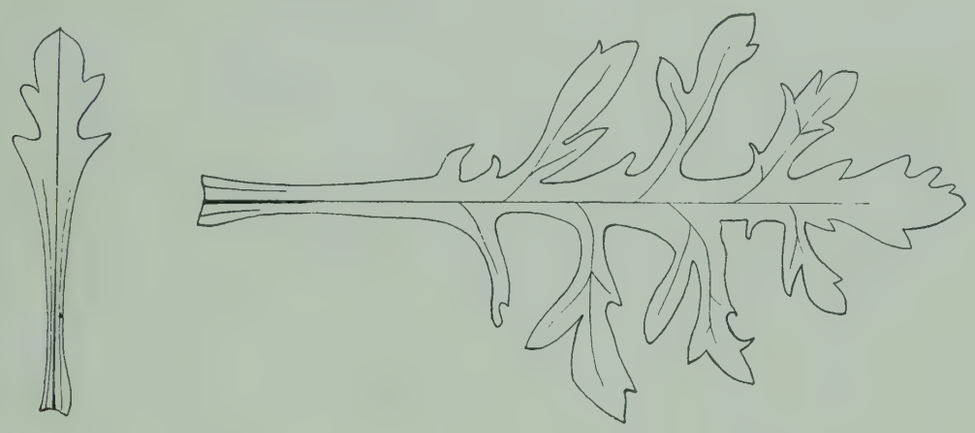
Figures 20, 21

Plants erect, 1–4 dm. tall, simple or few-branched from the base, paniculately much branched above; basal leaves oblanceolate, 1–5 cm. long, pinnately or irregularly bi-pinnately lobed and divided, tomentose; lower cauline leaves toothed or pinnately lobed, tomentose, not glandular; upper cauline leaves bract-like, entire, glandular; heads single at the ends of slender branchlets; corolla yellow with a purple band in the throat; style-branch 0.8 mm. long, appendage 0.17 mm. long, without a cusp; pappus bristles distinct.

Open hills from Santa Barbara Co. north through the Coast Ranges to Santa Clara Co., 250 to 1000 ft. July–Nov.

Localities.—Four miles south of Templeton, San Luis Obispo Co., J. T. Howell No. 3005 (type, H); along the highway four miles southwest of Orcutt, Santa Barbara Co., J. T. Howell No. 2998 (H); Paso Robles, San Luis Obispo Co., G. B. Grant, Nov. 9, 1897 (S); Priest

Valley, San Benito Co., W. Hickey, June 16, 1926 (H); Nacimiento River, thirteen miles west of Jolon, Santa Lucia Mts., Monterey Co., J. T. Howell No. 3011 (H); Santa Maria River bed, Eastwood No. 304 (CA); Tassajara Hot Springs, Santa Lucia Mts., Monterey Co., Dudley, July 1, 1901 (S); Tassajara Hot Springs, Elmer No. 3387 (S, Cl); along Carmel River, Monterey Co., Dudley, June 26, 1905 (S); Saratoga, Santa Clara Co., Dudley, Sept. 15, 1901 (S); Jasper Ridge, Santa Clara Co., Mallory, July 15, 1919 (S).



20 21

Figs. 20, 21. *L. germanorum* var. *tenuipes* J. T. Howell. Basal leaves, from type sheet. J. T. Howell No. 3005. × 1½.

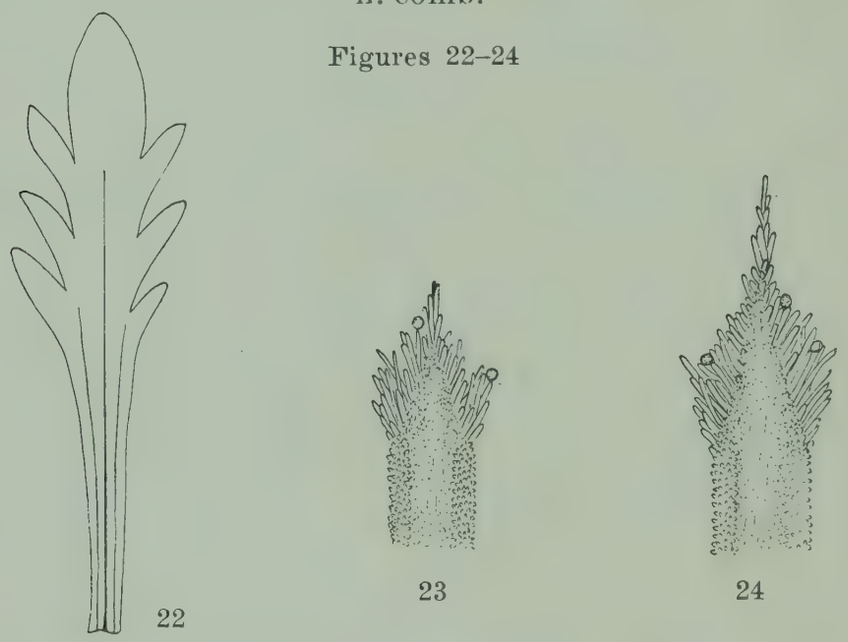
As indicated in the list of specimens cited above this variety embraces nearly all the yellow-flowered *Lessingias* of the south Coast Ranges except *L. germanorum* var. *parvula* and *L. germanorum* var. *vallicola,* the latter being rare in this region. (*Lessingia germanorum* var. *pectinata* is strictly a coastal sand hill form.) *Lessingia germanorum* var. *tenuipes* constitutes a polymorphic series of closely related taxonomic or genetic lines, scarcely distinguishable from each other in technical characters but varying irregularly in type of habit, color of stems, texture of leaves, character of tomentum, and disposition of glands. In common, all forms are rather low of stature (being under 4 dm. high), bear single heads at the ends of slender branchlets, have very short blunt style appendages, and have pappus bristles distinct. The plants growing at the type locality near Templeton are very distinctive with irregularly divided basal leaves, but it is believed that all forms in the variety are not so characterized. The plant collected near Orcutt is not strictly erect and has purple stems, in which characters it approaches the coastal variety *pectinata.* The plant from Priest Valley has even the basal leaves glabrate-glandular, and the form collected by the author in the Santa Lucia Mountains has only the margins of the cauline leaves glabrate-glandular, a distinguishing character of *L. germanorum* var. *vallicola.*

The gray-green herbage of the other specimens from the Santa Lucia Mountains and the specimen from the Santa Maria River approaches in a perplexing way that of *L. germanorum* var. *parvula* of subspecies *eu-tenuis*. The much-branched habit of the plant from Saratoga is not found in the type or in other forms of the variety.

The exact status of these forms cannot be learned until extended field observations have been made and exhaustive garden cultures have been arranged to cover the entire group. Then it will be known whether the whole is best accepted as one highly variable variety or as several closely related varieties.

f. **Lessingia germanorum** var. **glandulifera** (Gray) J. T. Howell n. comb.

Figures 22–24



22 23 24

Figs. 22–24. *L. germanorum* var. *glandulifera* J. T. Howell. 22, basal leaf, from garden cultures. × 3½; 23, appendage of style-branch. J. T. Howell No. 2981. × 50; 24, appendage of style-branch. J. T. Howell No. 3089. × 50.

Lessingia glandulifera Gray, Proc. Am. Acad., 17:207, 1882.

Plants 1–5 dm. high, cymose-paniculately branched, the ultimate branchlets generally numerous; herbage glabrate or tomentose, very glandular, the glandular secretion odorous and bitter; basal leaves spreading, oblanceolate, 2–6 cm. long, more or less tomentose, broadly obtuse to acute, margin pinnately lobed; cauline leaves oblongish to oblanceolate, 0.5–2.5 cm. long, acute, glandular, margin lobed or entire, the uppermost leaves 1.5–5 mm. long, apparently denticulate because of the large marginal glands; heads solitary, 20–30-flowered; involucre 5–8 mm. high, broadly turbinate, often closely subtended by the uppermost leaves; corollas yellow often with a brown band in the throat; style-branches 1–1.3 mm. long, appendage 0.35–0.65 mm. long with a prominent cusp extending beyond the dense tuft of hairs

or the appendage subulate; achene short- to long-turbinate, 2–3 mm. long; pappus 1.5–3 mm. long, the bristles free to the base, 30–37 in one or two series, light brownish.

Lower and southern California north to the Tehachapi Mts., east to the San Jacinto and San Ysidro mountains, 100 to 5500 ft. May–Oct.

Localities.—San Bernardino Valley, San Bernardino Co., S. B. and W. F. Parish, Aug., 1880 (type, G); near Fontana, San Bernardino Valley, San Bernardino Co., J. T. Howell, No. 4080 (H); Lower California, Orcutt, Oct. 7, 1882 (UC); Palomar, San Diego Co., T. S. Brandegee, Aug. 1, 1893 (UC); Boulevard, Laguna Mts., San Diego Co., MacGregor, July 30, 1916 (S); Warner's Hot Springs, San Diego Co., Coomb (CA); Pine Valley, Cuyamaca Mts., San Diego Co., J. T. Howell No. 2981 (H); Strawberry Valley, Mt. San Jacinto, Riverside Co., J. T. Howell No. 2909 (H); road to Hemet at 4500 ft., Mt. San Jacinto, Riverside Co., J. T. Howell No. 2929 (H); Coldwater and Cattle Canyons, San Gabriel Mts., Los Angeles Co., Peirson No. 1260 (P, H); Arroyo Seco, San Gabriel Mts., Los Angeles Co., G. B. Grant, Sept. 14, 1906 (UC); Claremont, Los Angeles Co., Baker No. 3444 (UC, S, Cl, CA); San Fernando, Los Angeles Co., J. T. Howell No. 3142 (H); Newhall, Los Angeles Co., J. T. Howell No. 3089 (H).

The present variety has not been reported from the coastal plains of southern California. It is probably not tolerant of the alkaline soil of that district for it appears to be confined to well drained, sandy soil of the mountains, hills, and alluvial fans to the north and east.

As in the preceding variety, var. *tenuipes,* considerable variation has been found in the specimens referred here, but the variation is of such a nature that it can scarcely be treated taxonomically. Moreover there appears to be but little relation between the special development of certain characters and the geographic or physiographic distribution of the variants. Although the rugged and irregular topography of southern California favors the development within a restricted area of plants marked by a definite character, the same factor permits the isolation of parallel strains in widely separated and physiographically unrelated geographic localities. This irregular distribution of similar variants, the almost ever-differing combinations of specialized characters, and the complete gradations in most of the character variations discourage a more detailed taxonomic treatment of this group than is given here. The data given on the length of the style appendage (p. 13) indicates the variability of that structure and the widely separated stations where appendages of equal length are developed. Some variation is shown in the lobing and shape of the basal leaves (the basal leaves of plants from Mount San Jacinto are nearly entire, from the Laguna Mountains deeply lobed), and the foliage also varies

in texture and amount of tomentum. The much-branched habit of the typical form occurring near San Bernardino approaches var. *ramulosissima* of subspecies *eu-lemmonii* and is very different from the slender few-branched plants found in the San Jacinto Mountains and at scattered stations throughout the range of the variety. The glands on the montane forms are noticeably reduced, but all forms are believed to have the usual bitter and odorous glandular secretion.

The type locality of *L. glandulifera* Gray as indicated on the label of the type specimen is "dry mesas, San Bernardino Valley," collected by the Parish brothers, August, 1880.

g. **Lessingia germanorum** var. **tomentosa** (Greene) J. T. Howell n. comb.

Figure 25

Lessingia tomentosa Greene, Leaf. Bot. Obs., 2:32, 1910.

Plants low in habit and compact, 10–12 cm. high; branchlets and leaves persistently white-tomentose or the margins of the upper leaves glabrate and glandular; leaves rather crowded, long-ovate to oblong; heads solitary; involucres 5 mm. high, broadly turbinate, the bracts erect or subsquarrose, with green glandular tips; flowers yellow, the outer corollas palmate; style-branches 2–2.5 mm. long, appendage 0.4–0.6 mm. long, triangular cuspidate or somewhat subulate; achene long-turbinate, 3 mm. long; pappus dark to light brown, 3 mm. long, bristles 38–43 in two series.



25

Fig. 25. *L. germanorum* var. *tomentosa* J. T. Howell. Appendage of style-branch, from part of type collection. U. C. Herb. No. 87920. × 50.

The only specimen examined was from the original collection: southwest part of the Colorado Desert, San Diego Co., Orcutt, Oct. 21, 1889 (UC).

This little known and distinctive plant is anomalous in habit and tomentum in subspecies *eu-glandulifera.* It would probably be better understood as a distinct subspecies but its relations are obscure through lack of sufficient herbarium material.

h. **Lessingia germanorum** var. **ramulosissima** (A. Nelson) J. T. Howell n. comb.

Lessingia ramulosissima A. Nelson, Univ. Wyo. Publ. Sci., 1:138, 1926.

Plants branching from the base or just above the base forming an intricately and much-branched, round-topped bush, 1–3 dm. high; herbage mostly glabrate and glandular (the glands similar to those of the species but more numerous); basal leaves and lower cauline leaves

oblanceolate to oblong, shallowly lobed or saliently toothed, rarely entire, tomentose; leaves of the many, filiform branchlets bract-like, numerous, often imbricate and passing into the bracts of the involucre; heads many, solitary, 7–13-flowered; involucres narrowly turbinate, 4 mm. high, the bracts loosely imbricate, somewhat spreading at the glanduliferous tip; style-branches 1.2–2 mm. long, appendage 0.7–1 mm. long; achene 1.5 mm. long; pappus bristles 1–2 mm. long.

Mohave Desert in Los Angeles, Kern, and San Bernardino counties north to Owens Valley, Inyo Co., 2000 to 4000 ft. June–Oct.

Localities.—Hinckley, San Bernardino Co., Jones No. 4078 (isotype, CA, Cl); Owens Valley at the mouth of Rawson Creek. Inyo Co., Duran No. 1929 (Duran, H); Lone Pine, Inyo Co., Jones, Aug., 1926 (Cl), Randsburg, Kern Co., K. Brandegee, July, 1913 (UC); between Mohave and Lancaster, Los Angeles Co., Peirson No. 1261 (P); Palmdale, Los Angeles Co., Elmer No. 3620 (UC, S, Cl).

The following series of specimens collected over a period of several months shows that the much-branched form described in the present variety is the matured form of a plant of very different appearance which is often mistaken for typical *L. germanorum* var. *lemmonii:* north entrance to Cajon Pass, San Bernardino Co., June 11, 1927, J. T. Howell No. 2493 (H); between Deadman's Point and Box S Ranch, Mohave Desert, San Bernardino Co., July 9, 1927, J. T. Howell No. 2673 (H); north entrance to Cajon Pass, B. D. Stark, Sept. 9, 1927 (H).

i. **Lessingia germanorum** var. **lemmonii** (Gray) J. T. Howell n. comb.

Lessingia lemmonii Gray, Proc. Am. Acad., 21:412, 1886.

Plants branching from the base or below the middle, 0.6–3 dm. high; herbage tomentose below, becoming glabrate and glandular above; leaves near the base up to 3.5 cm. long, oblong-obovate, entire or with several salient teeth; cauline leaves slender-ovate or oblong, glabrate beneath, thinly tomentose above, the margins entire but with wart-like glands; the uppermost leaves small and linear; heads solitary, 12–22-flowered; involucres broadly turbinate, 5–6 mm. high, the bracts loosely imbricate, slightly squarrose, glandular, narrowly oblong, inclined to obtuse; corollas yellow without purplish band in throat, the outer palmate; style-branch 1.3–2 mm. long, appendage 0.7–1 mm. long, slender-subulate; achenes 2 mm. long compressed-obovate; pappus 2–3 mm. long, brown, bristles 30–40, mostly free.

Santa Barbara, Ventura, and San Bernardino counties, California; north central Arizona; 1000 to 6000 ft. June–Sept.

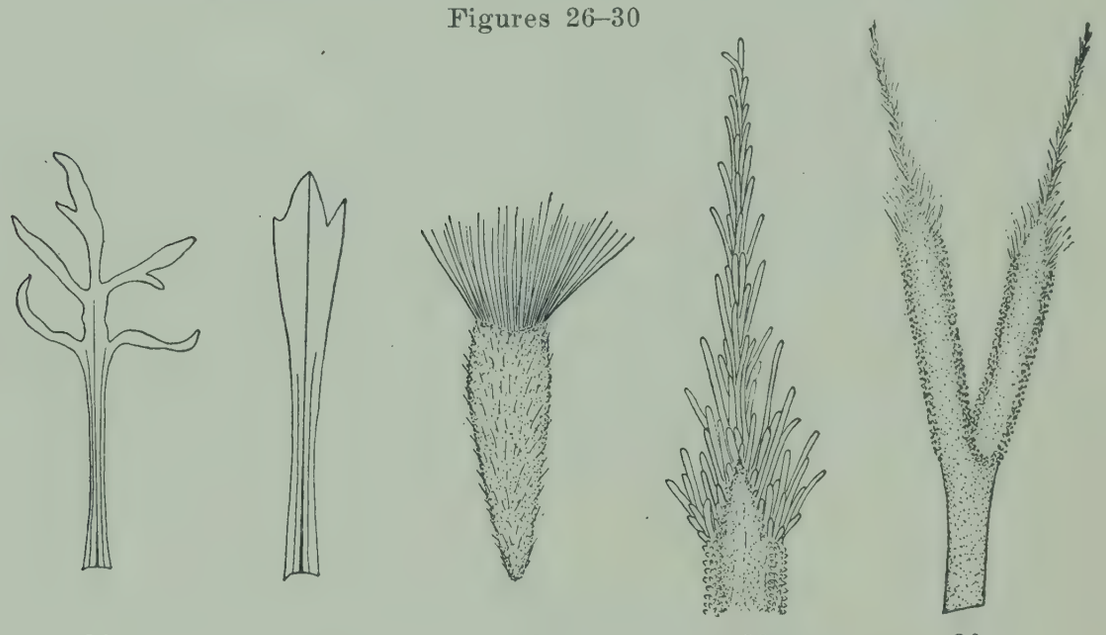
Localities.—Arizona: Ashfork, Lemmon, July, 1884 (isotype, specimen on lower half of sheet U. C. Herb. No. 87920, UC); Peach Springs, Lemmon, June, 1884 (UC). California: mesas, San Bernardino, San Bernardino Co., Parish (UC); one mile north of summit of Cajon Pass, San Bernardino Co., Johnston, Aug. 31, 1924 (Cl);

Mt. Pinos, Ventura Co., Hall No. 6621 (UC); Mt. Pinos, Ventura Co., Peirson No. 4229 (P, S, H); Mantau Ranch, Mt. Pinos region, Ventura Co., Dudley and Lamb No. 4725 (S, Cl); Cuyama Valley, thirty-eight miles west of Maricopa, northern Santa Barbara Co., Keck No. 485 (UC, Cl, H).

Lessingia lemmonii Gray is the only species of *Lessingia* having its type locality outside of California, it being at Ashfork in north central Arizona.

j. **Lessingia germanorum** var. **peirsonii** J. T. Howell n. var.

Figures 26–30



Figs. 26–30. *L. germanorum* var. *peirsonii* J. T. Howell. 26, basal leaf. × 1; 27, basal leaf. × 5; 28, achene and pappus. × 7½; 29, appendage of style-branch. × 50; 30, style-branches. × 25. All drawings of *L. germanorum* var. *peirsonii* are from the type sheet, Peirson No. 3550.

Plants 3–15 cm. high, either lower part simple and branched above or branched from dense basal rosette of leaves; herbage gray-green, closely matted-woolly, tomentum in part deciduous but not entirely so; glands on margins of upper leaves and involucral bracts; basal leaves 0.9–4.5 cm. long, the smaller ones entire or with one to several salient teeth, linear, the larger leaves pinnately divided, segments linear; cauline leaves 1–3.5 cm. long or less, linear to oblanceolate and oblong, entire or with pinnately arranged segments or teeth, passing into the glandular-margined, bract-like uppermost leaves; heads 6–17-flowered; involucre oblong-turbinate, 5–6 mm. high, the bracts erect, not imbricate, the outer foliaceous and tomentose; style-branches 1.8 mm. long, appendage 0.86–1 mm. long; achene 3–3.5 mm. long, turbinate-oblong; pappus 2 mm. long, bristles 22–27.

The west side of the Mohave Desert and bordering mountains from southern and eastern Kern Co. to northern Los Angeles Co.

Localities.—Kings Canyon, Liebre Mts., Los Angeles Co., Peirson No. 3550 (type, H, P, S); near Elizabeth Lake, 4000 ft., Liebre Mts., Munz No. 6936 (UC, Cl); Elizabeth Lake, Liebre Mts., Munz and Johnston No. 11154 (Cl); Oakgrove Canyon, Liebre Mts., Abrams and McGregor No. 317 (S); Frazier Mountain Park, southern Kern Co., J. T. Howell No. 3826 (the plants of this collection approach var. *lemmonii* in thinness of tomentum, H); southeastern Kern Co., Hall and Chandler No. 7373 (UC, Cl); Indian Wells Valley, Kern Co., Peirson No. 7331 (showing a much-branched habit not found in the type; P, H).

Lessingia germanorum var. *peirsonii* is readily distinguished from the related varieties in subspecies *eu-lemmonii* by the felt-like tomentum which clothes the branches and covers the exposed parts of the involucral bracts. The basal leaves of the plants in the type specimen have a distinctive shape but some variation is found in this character. Variation has also been found in the type of branching and in the thickness of the tomentum. With further field study this variety might be found to resemble in the number of minor variations the varieties *glandulifera* and *tenuipes* in subspecies *eu-glandulifera*.

2. **Lessingia nemaclada** Greene, Bull. Calif. Acad. Sci., ser. 1, 4:191, 1885

Figure 31

Lessingia leptoclada var. *microcephala* Gray, Proc. Am. Acad., 7:351, 1868. *L. ramulosa* var. *microcephala* Jepson, Man. Fl. Pl. Calif., 1041, 1925.

Plants 2–5.5 dm. high, branching from the base or simple below and branching above, the ultimate branchlets numerous and filamentous; basal leaves not known; leaves of branchlets scale-like, appressed, punctate- and stipitate-glandular; heads 3–6-flowered, solitary at the ends of the branchlets; involucres very slender-turbinate, 5–6 mm. high, the bracts erect, rather numerous and imbricate, stipitate-glandular; corollas all tubular or one or two palmate, purplish; style-branches 0.9–1.5 mm. long, appendage half as long, 0.44–0.7 mm. long, slender-subulate; achenes 3–4 mm. long; pappus of about twenty-five partly united bristles or of five simple or bristly, paleaceous awns, 1.5–3.5 mm. long.



Fig. 31. *L. nemaclada* Greene. Appendage of style-branch, from type sheet of *L. leptoclada* var. *microcephala* Gray, G. × 50.

31

Inner north Coast Ranges of Glenn and Colusa Cos.; foothills of the Sierra Nevada from Eldorado Co. to Tuolumne Co.; 1000 to perhaps 2500 ft. July–Sept.

Localities.—Sweetwater (Creek?), Eldorado Co., Curran, Aug., 1883 (type, CA, UC); Bear Mountain, Torrey in 1865 (type of *L.*

leptoclada var. *microcephala* Gray, G); Rawhide, Tuolumne Co., Williamson No. 155 (S, CA, Cl; approaches *L. nemaclada* var. *mendocina*); Epperson's, Colusa Co., Curran in 1884 (cotype of *L. nemaclada* Greene, CA); Mud Flat, Glenn Co., Heller No. 11522 (UC, S, CA); Antioch, Contra Costa Co., K. Brandegee in 1883 (UC: this locality must be verified; the specimen is probably part of the collection made the same year by Mrs. Brandegee [who was then Mrs. Curran] at Sweetwater, Eldorado Co.).

"Sweetwater," the type locality of *L. nemaclada* Greene is undoubtedly in the vicinity of Sweetwater Creek in the Sierra foothills of Eldorado County at an elevation of about 1000 feet. The type locality of *L. leptoclada* var. *microcephala* Gray could not be determined exactly but is probably in the vicinity of Bear Valley, Mariposa County. This was concluded after studying Torrey's route in California in 1865.

Typical *L. nemaclada* is known only from a few specimens from two districts on either side of the Great Valley. Although very distinctive with its filiform stems, reduced leaves, and small heads it represents a highly specialized form of the widespread var. *mendocina*. The two might be better understood as a single, variable unit, but here typical *L. nemaclada* is believed to be sufficiently distinct to warrant recognition apart from var. *mendocina*.

a. **Lessingia nemaclada** var. **mendocina** (Greene) J. T. Howell n. comb.

Lessingia mendocina Greene, Leaf. Bot. Obs., 2:28, 1910. *L. cymulosa* Greene, Leaf. Bot. Obs., 2:30, 1910. *L. fastigiata* Greene, Leaf. Bot. Obs., 2:31, 1910. *L. paleacea* Greene, Leaf. Bot. Obs., 2:31, 1910.

Plants 1–3 (or to 6) dm. tall, branched from the base or simple below and much-branched above; the ultimate branchlets very slender with few bract-like leaves, these punctate- and stipitate-glandular; heads 4–8-flowered, solitary or rarely 2–4-clustered; outer corollas palmate; style-branches 1.3–2 mm. long, appendage subulate, 0.5–0.9 mm. long; pappus bristles nearly distinct, 14–23, or usually united into five bristly sets paleaceous at the base, sometimes reduced to five awns.

Sierra Nevada foothills from Fresno Co. north to Siskiyou Co., thence west to Humboldt Co. and south to Mendocino and Lake Cos., 500 to 2100 ft. June–Sept.

Localities.—Near Mendocino, Mendocino Co., H. E. Brown No. 940 (type of *L. mendocina* Greene, US); Chowchilla Post Office, Mariposa Co., Ward, Oct. 10, 1895 (type of *L. cymulosa* Greene, US); Middle Fork of Cottonwood Creek, Fresno Co. (Tehama Co. on label), Ward, Sept. 16, 1895 (isotype of *L. paleacea* Greene, US); Sweetwater, Eldorado Co., K. Brandegee (UC); Butte Co., R. M. Austin, in 1883

(UC); Delta, Shasta Co., Heller No. 11746 (UC, CA, S); Redding Shasta Co., E. L. Greene, Sept., 1889 (UC); Redding, Shasta Co., J. T. Howell No. 2297 (seedlings, H); Dunsmuir, Siskiyou Co., Heller No. 12494 (UC, CA); Burnt Ranch, Trinity Co., Tracy No. 5218 (UC); Klamath River, Humboldt Co., Chandler No. 1503 (UC, S); Scott Valley, Siskiyou Co., Butler No. 1827 (UC, S, Cl); Castella, Shasta Co., Eastwood No. 1361 (CA); Round Valley, Mendocino Co., Jepson, July, 1897 (J); Spy Rock, Mendocino Co., Tracy No. 4858 (UC); Bartlett Springs, Lake Co., Augsburg, Aug., 1920 (CA).

The examination of the type specimens of *L. mendocina, L. cymulosa,* and *L. paleacea* has shown that these species were described from plants which differ mainly in habit but it is found that they are not sufficiently distinct to be named as separate varieties.

The type specimen of *L. fastigiata* Greene which is "from the foothills of the Sierra near Chico, by Mrs. R. M. Austin, 1896," has not been seen. From the type description and from the character of specimens collected in the vicinity of the type locality, *L. fastigiata* is believed to be the same as the present variety. The specimen collected by Chandler in Humboldt County which is referred to with some doubt as a cotype of *L. fastigiata* by Greene is *L. nemaclada* var. *mendocina.*

According to Greene, as recorded in the type description, the type specimen of *L. paleacea* was collected by L. F. Ward on the Middle Fork of Cottonwood Creek in Fresno County, September 16, 1895. The label on the type sheet was written in ink except for "Tehama Co." which was written in pencil after the words "Cottonwood Creek." To determine on which Cottonwood Creek the specimen was collected, other collections by Ward for the middle part of September, 1895, will have to be seen.

b. **Lessingia nemaclada** var. **albiflora** (Eastwood) J. T. Howell n. comb.

Figures 32, 33

Lessingia albiflora Eastwood, Bull. Torr. Bot. Club, 32:217, 1905. *L. glandulifera* var. *albiflora* Jepson, Man. Fl. Pl. Calif., 1041, 1925.

Plants branching from the base, or simple below and divaricately branching above, 1.5–3 dm. high; basal leaves 3–5 cm. long, oblong-oblanceolate, serrate, without glands, persistently flocculent-tomentose on both faces; cauline leaves ovate, 0.5–2 cm. long, cordate-clasping, carinate, strongly acruate-recurved, mucronate, densely tomentose above, glabrate beneath and glandular; the leaves of the ultimate branchlets bract-like, appressed, glandular; heads solitary at the ends

of the branchlets 6–8-flowered; involucres narrowly turbinate, 5 mm. high, the bracts rather few, with squarrose, granulous-glandular tips; corollas white, often with a purple throat, or the lobes varying from very pale lavender and white to purplish on one plant; style-branches 1–1.9 mm. long, appendage cuspidate or shortly subulate, 0.36–0.56 mm. long; achenes 3–4 mm. long, somewhat compressed; pappus light brownish, the bristles distinct, 28–33, up to 3 mm. long; cotyledons without callous grain at apex.



32



33

Figs. 32, 33. *L. nemaclada* var. *albiflora* J. T. Howell. 32, cotyledon, from garden cultures. × 5; 33, appendage of style-branch. Hall No. 12245. × 50.

From the inner south Coast Ranges in southern Monterey Co. south and east to the Tehachapi Mts. and Sierra Nevada foothills in Kern Co., 1000 to 3000 ft. Sept.–Oct.

Localities.—Near Tejon Ranch, Kern Co., Eastwood, Oct. 3, 1894 (type, CA); Parkfield, Monterey Co., Hall No. 12245 (UC, H); three miles north of summit of Parkfield Grade, western Fresno Co., Keck No. 471 (UC, Cl, H); Kern River road between Bakersfield and Bodfish, Kern Co., Abrams No. 5354 (S).

The type locality of *L. albiflora* Eastwood is on the outwash plains of the southern San Joaquin Valley between Rose Station and Bakersfield in Kern County.

3. **Lessingia leptoclada** Gray, Proc. Am. Acad., 7:351, 1868

Figures 34–42

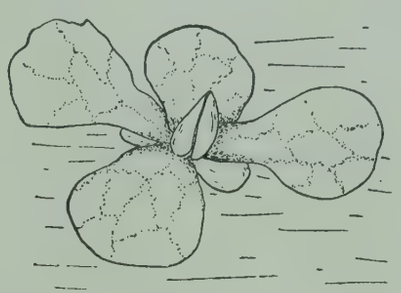
Lessingia leptoclada var. *typica* Gray, *loc. cit.* *L. leptoclada* var. *tenuis* Gray, *loc. cit.*

Plants erect, generally simple at the base, 3–6 dm. tall or depauperate forms as small as 2.5 cm. tall; herbage woolly-pubescent or glabrate, the upper cauline leaves punctate-glandular; basal leaves broadly oblanceolate or spatulate, 0.8–5 cm. long, conspicuously reticulate-veined, margin with 2–6 salient, acute teeth; cauline leaves broadly sessile, oblongish or oblong-oblanceolate, margin serrate or entire, 2.5–4 cm. long, passing into the small leaves of the slender branchlets; heads solitary or 2–5-glomerate, 12–22-flowered or as few as 6-flowered; involucres broadly turbinate, 0.6–1 cm. high, the bracts

short- to long-oblong, silvery-woolly, less glandular than the leaves, appressed or the extreme tip slightly squarrose, the tips of inner series tinged with lavender; corollas lavender-blue, outer corollas palmate; style-branches 0.8–2 mm. long, appendage 0.3–0.6 mm. long, with or without a cusp; achene oblong or narrowly turbinate, 3.5 mm. long; pappus bristles straw-brown to dark brown, in one or two series, 18–40, 4–7 mm. long, distinct or rarely united at the base into five or more



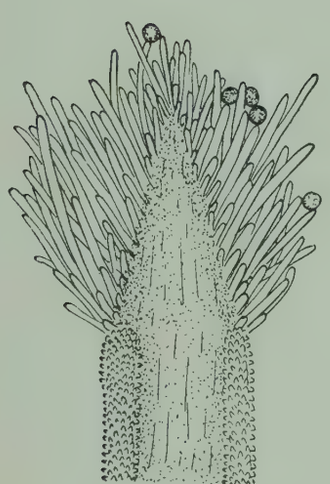
34



35



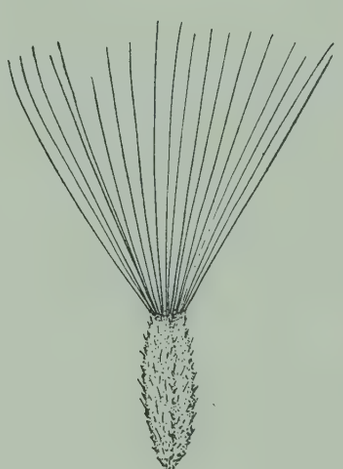
36



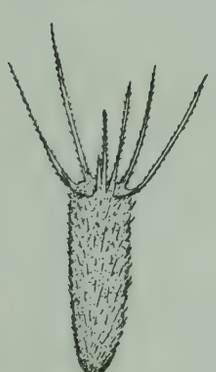
37



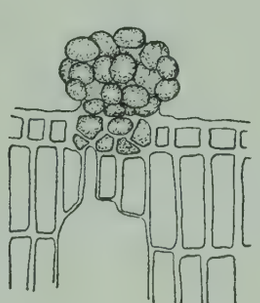
38



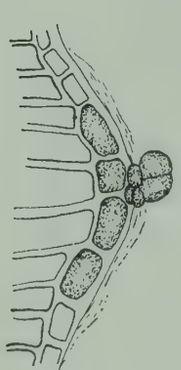
39



40



41



42

Figs. 34–42. *L. leptoclada* Gray. 34, cotyledon, from garden cultures. × 5; 35, seedling habit, from garden cultures. × 2½; 36, basal leaf. Mason No. 2183. × ¾; 37, appendage of style-branch. J. T. Howell No. 3069. × 75; 38, appendage of style-branch. J. T. Howell No. 3086. × 75; 39, achene and pappus. Keck in 1926, H. × 5; 40, achene and pappus. U. C. Herb. No. 87934. × 10; 41, 42, punctate glands on leaves. Mason No. 2183. × 200.

bristly sets; cotyledons obtuse or emarginate, without a callous grain at apex, coriaceous in appearance, upper surface rugulose-veined.

Open slopes and valley lands of the Sierra Nevada, 1000 to 6200 ft., from Tulare Co. north to Eldorado Co. July–Sept.

Localities.—Riverton, Eldorado Co., K. Brandegee, Aug., 1914 (UC); Pioneer, Amador Co., Hansen No. 781 (UC, Cl); Hog Ranch, Tuolumne Co., Mason No. 2183 (M, H); Yosemite Valley, Mariposa Co., Bolander No. 4924 (an isotype[?], UC); foot of Yosemite Falls, Yosemite Valley, Mariposa Co., J. T. Howell No. 4091 (seedlings, H); Wawona, Mariposa Co., J. T. Howell No. 221 (H); North Fork of the Kings River, Hall and Chandler No. 439 (UC); near Kanawyer's, South Fork of the Kings River, Fresno Co., Peirson No. 1257 (P); five miles below Three Rivers, Tulare Co., J. T. Howell No. 3069 (H); Black Oak Point, Sequoia National Park, J. T. Howell No. 3086 (H).

As in other large species of the genus, *L. leptoclada* develops a large number of forms. The heads are often solitary but forms are just as numerous in which the heads are glomerate at the ends of the branchlets. The length and shape of the involucres are exceedingly variable, passing from short, hemispheric forms to longer, broadly turbinate or narrowly turbinate forms. There is also much variation in the appendage of the style-branch, which passes by many intermediate forms from a truncate, penicillate tuft to a cuspidate or short-subulate appendage. As a rule there is little tendency for the pappus bristles to unite at the base but several forms were seen with the bristles united into five or more bristly awns.

The following specimens are marked by the small size of the involucres. Because of complete intergrading with the more typical form of the species and since great variation is found on single plants, a new variety was considered untenable: between Eldorado and Placerville, Eldorado Co., Heller No. 12257 (CA, S); St. Lawrence, Eldorado Co., Jones No. 3618 (Cl, CA); White and Hatch's, Mariposa Co., Congdon, Sept., 1883 (No. 87934, UC; on this sheet are near-extremes of variation of size of involucres presumably from the same locality); Middle Tule River, Tulare Co., Purpus No. 1477 (UC); Tule River below Nelson, Peirson No. 1259 (P). The largest involucres measured are on specimens collected by K. Brandegee, between Fyffe and Camino, Eldorado Co., in 1914 or 1915 (UC). Two specimens in which the pappus is much reduced are: Jackson, Amador Co., Michener and Bioletti, Aug., 1893 (UC); Yosemite Valley on the Inspiration Point road, Kennedy No. 3008 (UC).

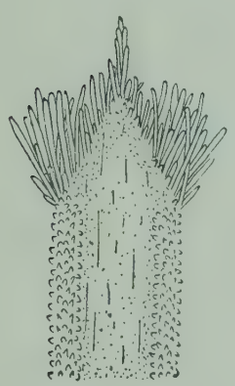
This species was described by Gray from specimens collected by H. N. Bolander on the sandy floor of Yosemite Valley in Mariposa County.

4. **Lessingia virgata** Gray, Benth. Pl. Hartw., 315, 1849

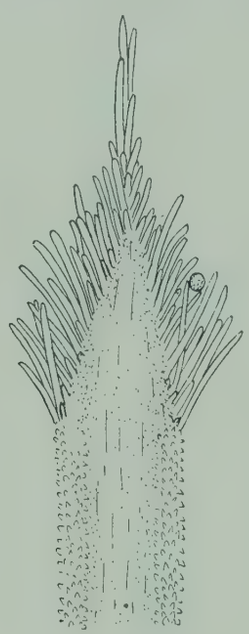
Figures 43, 44

Lessingia subspicata Greene, Leaf. Bot. Obs., 2:29, 1910.

Plants erect, 4–6 dm. high, branching from near the base, the branches and branchlets virgate, somewhat spreading, bearing numerous erect appressed leaves; basal leaves and lower cauline leaves unknown; upper cauline leaves 1–2.5 cm. long, broadly ovate to oblong-ovate, acute, entire, or with one to several teeth, passing above into bract-like leaves; the uppermost leaves 0.5–1.5 cm. long, ovate, acute, entire, densely white-woolly or the lower side more or less glabrate,



43



44

Figs. 43, 44. *L. virgata* Gray. 43, appendage of style-branch. K. Brandegee at Brighton, UC. × 50; 44, appendage of style-branch. T. S. Brandegee at Red Bluff, UC. × 50.

glands punctate and stipitate; inflorescence generally spicate; heads 3–6-flowered, solitary and sessile in the axils of the leaves; involucres slender-turbinate, 5–7 mm. high, the bracts few, well imbricated, the purple tips erect or slightly squarrose, glandular; corollas lavender, tubular or palmate; style-branch 1.2 mm. long, appendage 0.3–0.8 mm. long, cuspidate to slender-subulate; achenes 2–2.5 mm. long, 3-angled, rounded dorsally, strongly carinate ventrally; pappus of 27–32 bristles, 2.5 mm. long and tending to become united at the base.

Foothills of the Sierra Nevada and the upper Sacramento Valley, 100 to 1000 ft., from San Joaquin Co. to Tehama Co. June–Oct.

Localities.—Buffalo Ranch, ten miles east of Oroville, Butte Co., Leiberg, Sept. 28, 1900 (type of *L. subspicata* Greene, US); Red Bluff, Tehama Co., T. S. Brandegee, Sept. 20, 1892 (UC); Oroville, Butte Co., Heller No. 11762 (UC, S, CA); Roseville, Placer Co., Heller No. 12275 (S, CA); between Shingle Springs and Clarksville, Eldorado Co., Heller No. 12274 (S, CA); Brighton, Sacramento Co., K. Brandegee in 1883 (UC); Live Oaks, San Joaquin Co., Rattan, Oct., 1880 (S); Stockton, San Joaquin Co., Parry in 1881 (UC).

Lessingia virgata Gray was first collected by Charles Pickering, naturalist with the section of the United States Exploring Expedition which visited California in 1841 (see Gray, 1874). The plant was found between August 23 and September 9, "prope Nueva Helvetia," New Helvetia being the name of the establishment of Captain Sutter, a Swiss, at the junction of the Sacramento and American rivers, the site of the present city of Sacramento.

The following data give an idea of the great variation in length of style appendage found within the species *L. virgata:*

Brighton, Sacramento County, K. Brandegee (UC)	0.3 mm.
Oroville, Heller No. 11762 (UC)	0.3 mm.
Live Oaks, Rattan in 1880 (S)	0.4–0.5 mm.
Buffalo Ranch, Leiberg in 1900 (US)	0.7 mm.
Red Bluff, T. S. Brandegee in 1892 (UC)	0.8 mm.

Lessingia subspicata Greene is a form of *L. virgata* in which the heads are arranged in a spicate manner along some of the branchlets and in a glomerate manner at the ends of others.

a. **Lessingia virgata** var. **glomerata** (Greene) J. T. Howell n. comb.

Lessingia glomerata Greene, Leaf. Bot. Obs., 2:30, 1910.

Plants 2–4 dm. high, simple nearly to the top or branching from near the base; lower cauline leaves somewhat glabrate beneath, woolly above, oblong-oblanceolate, 1–2 cm. long; upper leaves bract-like, numerous and imbricate near the ends of the branchlets, spinescent-acute, woolly above, punctate-glandular and conspicuously woolly below; heads "5–10-flowered," solitary or 2–6 in a glomerule, or rarely axillary along the branchlets; involucre slender-turbinate, 6 mm. high, the bracts erect or subsquarrose, not sharply acute, with small stipitate glands at the apex; style-branch 1.7–2 mm. long, appendage subulate, 0.7–0.9 mm. long; achene flattened, 3 mm. long; pappus bristles 4 mm. long, dark brown, 15–20 in one series, distinct or tending to unite at the base.

Plains and hills from Butte Co. north to Siskiyou Co., 500 to 2000 ft.

Localities.—Sacramento Valley ("probably near Chico" according to E. L. Greene), Parry in 1882 (type of *L. glomerata* Greene, US); Chico, Butte Co., Parry in 1881 (S); Dunsmuir, Siskiyou Co., G. B. Grant, Sept., 1902 (S; the large specimen on the upper half of sheet No. 61686, UC).

In habit this variety resembles *L. nemaclada* var. *mendocina* more than *L. virgata.* But because of the technical characters of the leaves, amount of tomentum on the lower sides of the leaves, and character of the involucres it is believed to be closer to *L. virgata.* The

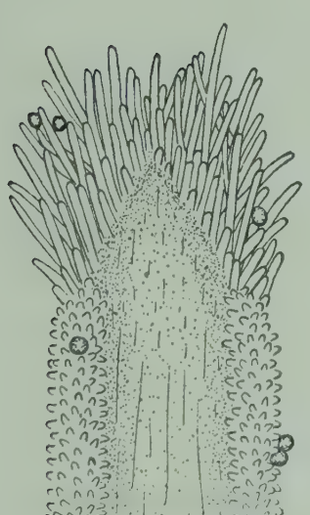
glomerate inflorescence is interpreted to be a highly reduced and abbreviated form of the spicate inflorescence which is found in typical *L. virgata.* However, some reduced forms of *L. virgata* approach var. *glomerata* in habit such as the specimens collected by Rattan at Fair Oaks in 1880. And also in some very robust specimens such as Leiberg's specimen from Buffalo Ranch, the heads on many of the branchlets are not spicately arranged but are glomerate at the ends of the branchlets. From the data on the length of the style appendage given under *L. virgata,* it is seen that the increased length of the style appendage in var. *glomerata* is the culmination of a tendency found in the species.

5. **Lessingia nana** Gray, Benth. Pl. Hartw., 315, 1849

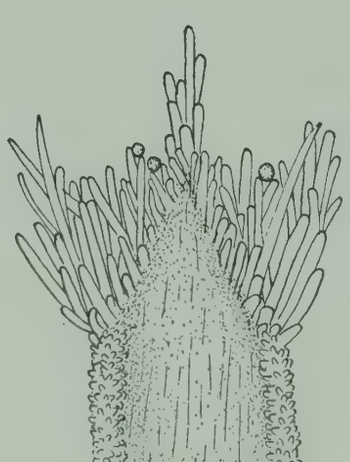
Figures 45–47



45



46



47

Figs. 45–47. *L. nana* Gray. 45, punctate gland on leaf. U. C. Herb. No. 148610. × 1000; 46, appendage of style-branch. U. C. Herb. No. 65510. × 100; 47, appendage of style-branch. U. C. Herb. No. 33164. × 100.

Lessingia nana var. *caulescens* Gray, Syn. Fl. N. Am., 1, pt. 2:163, 1884. *L. parryi* Greene, Bull. Calif. Acad. Sci., ser. 1, 4:191, 1885.

Plants acaulescent, 1–2 cm. high, or plants caulescent, the branches stout, decumbent to erect, 2.5–10 cm. long; herbage pale green or white with long densely matted white wool, all parts becoming glabrate or nearly so with age; the upper leaves punctate-glandular beneath; basal leaves spreading, linear-oblanceolate, acute, subentire to coarsely serrate, 0.8–5 cm. long or rarely the petiole-like base itself 5 cm. long; cauline leaves oblong-linear to ovate, 0.5–3.5 cm. long; heads conspicuous, 0.8–1 cm. high, 12–18-flowered, axillary or solitary to glomerate at the ends of branchlets; involucre slender-urceolate, the outer bracts herbaceous, acute, mucronate, the tips woolly, the inner bracts with long, white, crustaceous tips, these exceeding the flowers even at time of anthesis; corollas rose color in dry material; style-branch 1–1.8 mm. long, appendage 0.22–0.38 mm. long, cusp generally evident or rarely absent; achenes broadly oblong to turbinate, slightly flattened, 2–3 mm. long; pappus showy, bright to dark rose-red or sometimes light rufous-brown, the bristles 50–70 in two series, up to 7 mm. long, distinct to the base.

Foothills of the Sierra Nevada from Kern to Eldorado Co., 100 to 2700 ft. July–Sept.

Localities.—Kern Co., Greene in 1881 (CA, type of *L. parryi* Greene; UC, S); Mariposa, Mariposa Co., Congdon, Aug. 1, 1893 (UC, S); San Andreas, Calaveras Co., Hansen No. 388 (UC, Cl); Galt, Sacramento Co., Michener and Bioletti, Aug. 14, 1893 (UC); Ione, Amador Co., Braunton No. 1157 (UC, S); Chico, Butte Co., Clemens, Oct. 1922 (CA); Red Bluff, Tehama Co., Wickes, July 25, 1917 (CA).

The first specimens of *L. nana* were collected by Charles Pickering of the Wilkes Expedition between August 23 and September 9, 1841, "in California prope Nueva Helvetia"—Nueva Helvetia being the early place name of Sacramento.

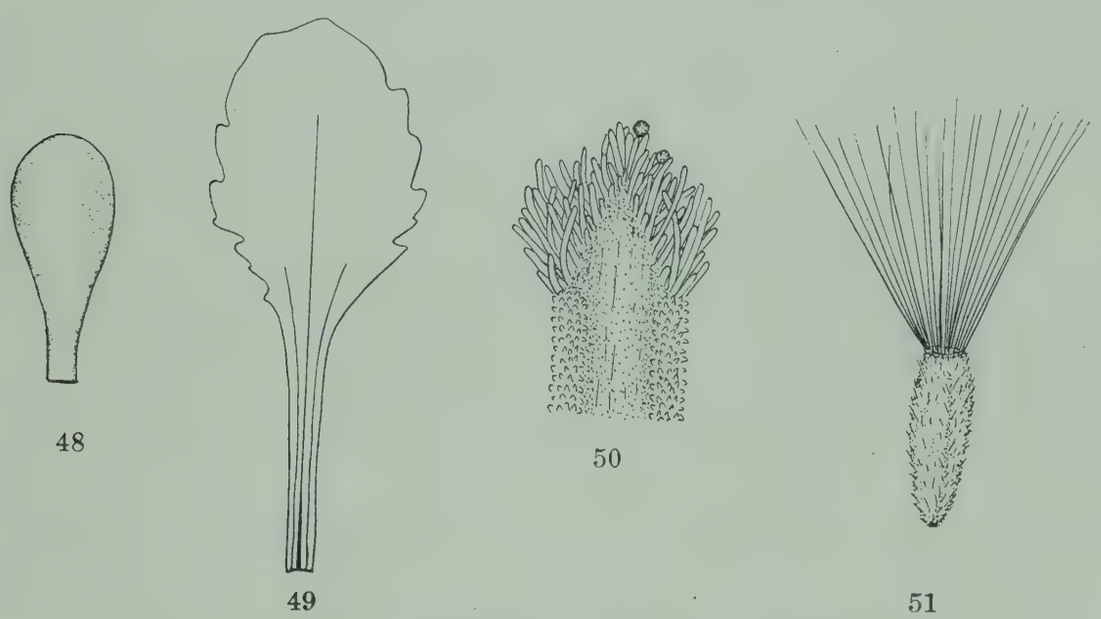
This *Lessingia* is very distinctive with its white, woolly herbage, bony, white inner involucral bracts and bright red or ferruginous pappus. Although sometimes a very low dwarf, it generally develops short stems and from extreme types of the latter have been described the two forms whose names are given as synonyms above. Much variability is found in the character of the style appendage, some appendages showing no cusp at all, some with a cusp more or less hidden in the penicillate tuft, and others with a well developed and conspicuous cusp extending well beyond the tuft.

6. **Lessingia ramulosa** Gray, Benth. Pl. Hartw., 314, 1849

Figures 48–51

Lessingia bicolor Greene, Leaf. Bot. Obs., 2:28, 1910.

Plants up to 4.5 dm. tall, with many branches from the densely leafy base, these strict or slightly divergent and much surpassing the short, main shoot; herbage often becoming densely glandular; basal leaves oblong-oblanceolate, broadly sessile or narrowed to a slender petiole-like base, 3–5 cm. long, acute, serrate; cauline leaves 0.5–1.5 cm. long, round-ovate to oblong, carinate, acute, entire, becoming scale-



Figs. 48–51. *L. ramulosa* Gray. 48, cotyledon, from garden cultures. × 2½; 49, basal leaf, from garden cultures. × ¾; 50, appendage of style-branch, from type sheet, G. × 50; 51, achene and pappus. J. T. Howell No. 3053. × 5.

like on flowering branchlets, all leaves with persistent copious white tomentum on upper side; inflorescence cymose-paniculate; heads single at end of branchlets, 3–13-flowered; involucre turbinate, 5–7 mm. high, bracts imbricate, the tips slightly spreading, the outer herbaceous, the inner herbaceous at apex and glandular, the glands hair-like or capitate; corollas rose color or pale pink, drying purplish, funnelform, the outermost only slightly enlarged and not palmate-reflexed; style branch 1.3 mm. long, appendage 0.24–0.3 mm. long, no cusp present; achenes oblong-turbinate, 3 mm. long; pappus bristles 25–37, mostly free, rarely several united at the base; cotyledons obtuse, without callous grain at apex.

Hills and mountains of Solano Co., north to Sonoma, Lake, and Mendocino counties, 300 to 2500 feet. Aug–Nov.

Localities.—Near Sonoma, Sonoma Co., Hartweg No. 1769, Sept., 1846 (type, G); Santa Rosa, Sonoma Co., Heller No. 6049 (isotype of *L. bicolor* Greene, UC, CA, Cl); hills southeast of Santa Rosa, Sonoma Co., J. T. Howell No. 2250 (H); Pope Valley, Napa Co., Bolander No. 2617 (UC); Scott's Valley, Lake Co., Tracy No. 2370 (UC, Cl);

near Upper Blue Lakes, Lake Co., Peirson No. 6351 (P, Cl); Cordelia, Solano Co., Sept. 25, 1893, Jepson (J); Anderson Valley, Mendocino Co., J. T. Howell No. 3053 (H); Laytonville, Mendocino Co., Eastwood No. 9334 (CA).

Lessingia ramulosa Gray was first collected near Sonoma, in September, 1846, by Theodor Hartweg, in the service of the London Horticultural Society. The type locality is given "In planitie prope Sonora." The locality is not Sonora but Sonoma. This was proved by tracing Hartweg's travels in California as set forth in his Journal (Hartweg, 1847, 1848; Jepson, 1897).

a. **Lessingia ramulosa** var. **adenophora** (Greene) Gray, Syn. Fl. N. Am., ed. 2, 1, pt. 2:446, 1886

Figure 52

Lessingia adenophora Greene, Bull. Calif. Acad. Sci., ser. 1, 4:190, 1885.

Similar in habit to the species but somewhat smaller; herbage more conspicuously glandular; upper leaves tomentose on both sides, the margins of the lower side glabrate and intensely glandular or rarely the lower side entirely glabrate; outer corollas not palmate; style-branches 0.9–1 mm. long, appendage 0.25–0.3 mm. long; achenes with pappus bristles united into five bristle-tipped awns or the awns simple and paleaceous.

Mountains from Napa Co. to northern Lake Co. and western Colusa Co., 1000 to 3000 ft. July–Sept.

Localities.—Epperson's, Colusa Co., Curran in 1884 (type of *L. adenophora* Greene, CA); Cobb Mt., Lake Co., Tracy No. 2245 (UC); Langtry Ranch, Lake Co., K. Brandegee, Aug. 16, 1911 (UC, S, Cl); Butt Valley road between Pope Valley and Middletown, Lake Co., J. T. Howell No. 3052 (H); Knoxville, Napa Co., Jepson, July, 1892 (J); Howell Mt., Napa Co., Tracy No. 2225 (UC).



52

Fig. 52. *L. ramulosa* var. *adenophora* Gray. Achene and pappus. J. T. Howell No. 3052. × 5.

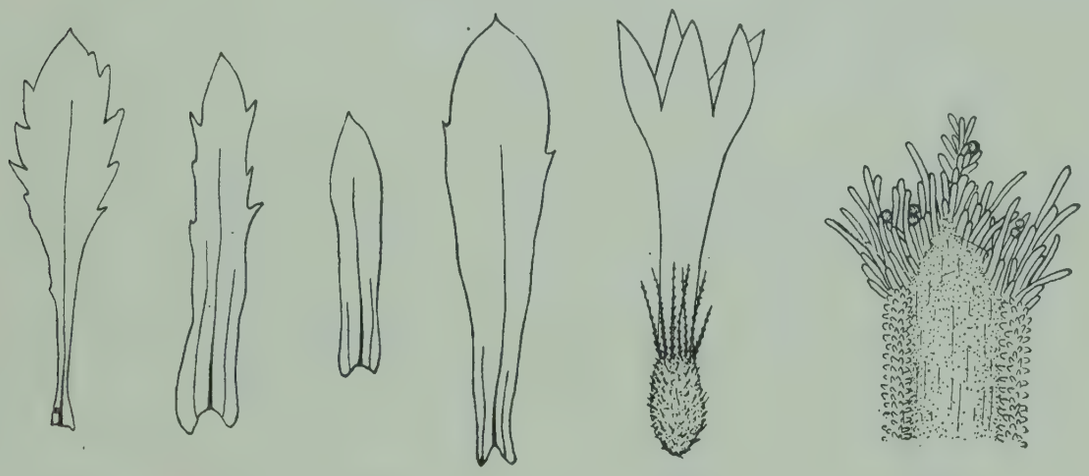
This variety is not based alone on the character of the pappus for in this work the modification of the pappus, striking as it is, is not held to be a varietal character since it occurs in varying degree in nearly every species. The habit, the character of the tomentum on the cauline leaves, and the more glandular herbage, as well as the paleaceous pappus, serve to distinguish the present variety from the species. Intermediate forms have been noted, among which are: Hullville, Lake Co., Heller No. 6033 (UC, CA, S, Cl); Howell Mt., Napa Co., Jepson No. 1732*A* (J). In these the pappus bristles were distinct but the plants are close to the variety because of the other characters.

b. **Lessingia ramulosa** var. **micradenia** (Greene) J. T. Howell n. comb.

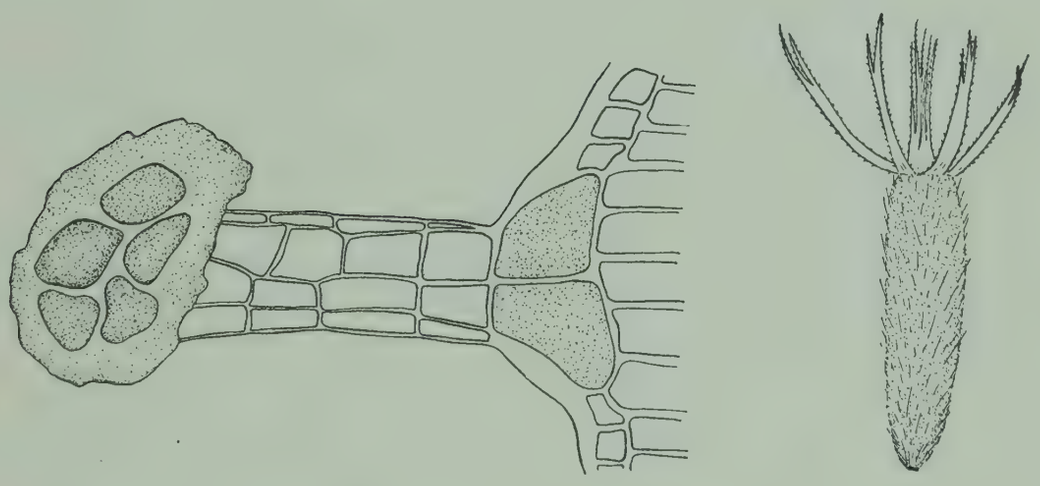
Figures 2, 3, 53–60

Lessingia micradenia Greene, Leaf. Bot. Obs., 2:28, 1910.

Plants unbranched from the base, divaricately and paniculately much branched from near the middle; heads narrowly turbinate, 5–10-flowered; outer corollas not palmate; style-branch 0.75–1 mm.



53 54 55 56 57 58



59 60

Figs. 53–60. *L. ramulosa* var. *micradenia* J. T. Howell. 53, basal leaf. × 1; 54, 55, 56, cauline leaves. × 1; 57, an outermost flower of a head. × 5; 58, appendage of style-branch. × 50; 59, glandular hair. × 500; 60, achene and pappus. × 10. All drawings of *L. ramulosa* var. *micradenia* are from Mason No. 2233.

long, appendage 0.26 mm. long, cusp evident; achene 2–4 mm. long; pappus becoming united into five simple paleaceous awns.

Hills of Marin Co. in the region just to the north of Mt. Tamalpais, 200 to 700 ft. Sept.

Localities.—Mt. Tamalpais, Marin Co., Jepson, Sept. 9, 1892 (J); Phoenix Lake, Marin Co., J. T. Howell No. 2191 (H) and No. 2360

(seedlings, H); Phoenix Lake, Marin Co., Mason No. 2233 (M, H); Liberty's, Marin Co., Eastwood, Sept. 26, 1915 (CA); Alpine, Marin Co., Sutliffe, Sept. 14, 1919 (CA).

The type locality of *L. micradenia* Greene is Mount Tamalpais, Marin County.

7. **Lessingia hololeuca** Greene, Fl. Franciscana, 377, 1897

Figures 61–67

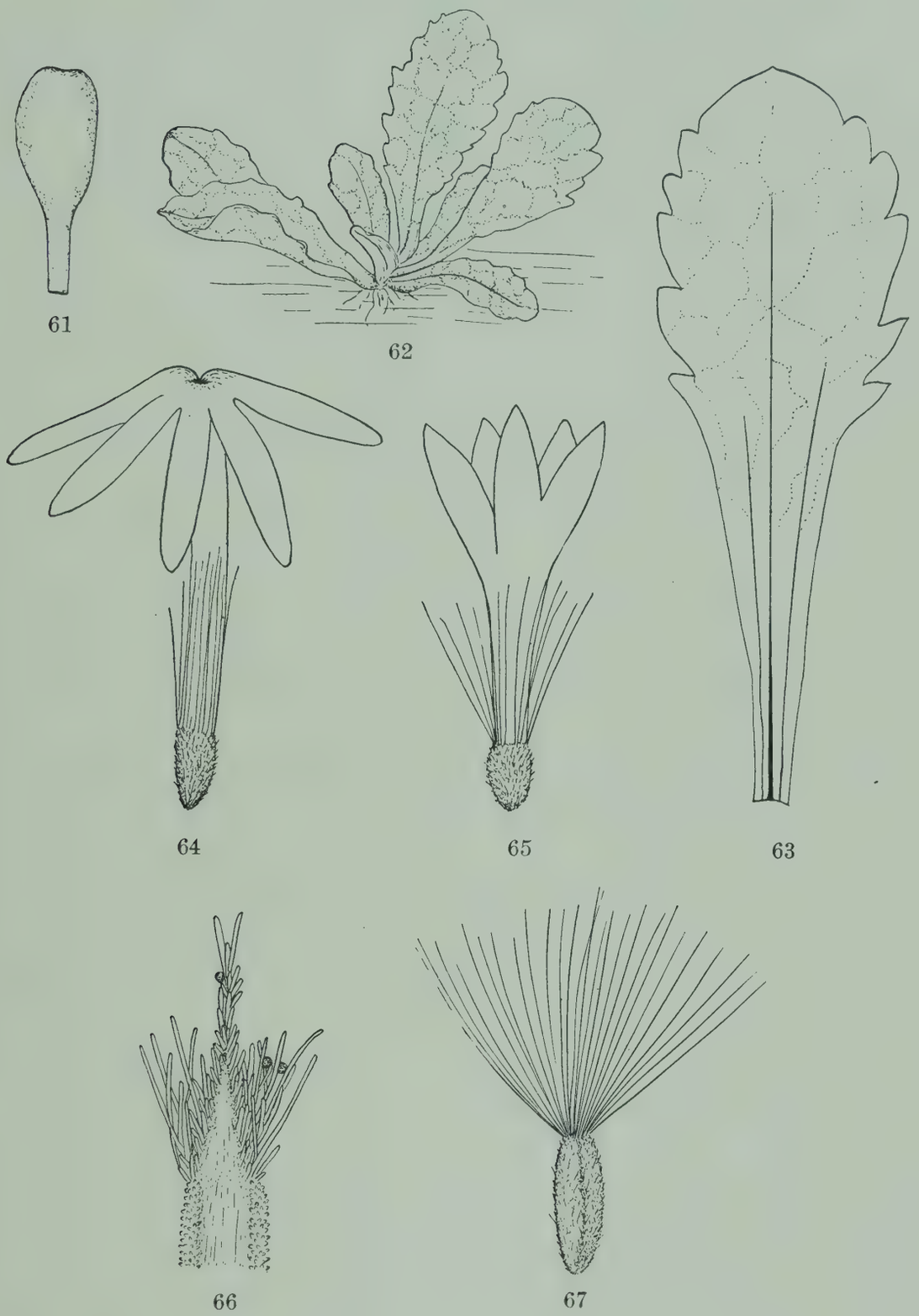
Lessingia bakeri Greene, Leaf. Bot. Obs. 2:27, 1910. *L. imbricata* Greene, Leaf. Bot. Obs., 2:29, 1910. *L. leptoclada* var. *hololeuca* Jepson, Man. Fl. Pl. Calif., 1040, 1925.

Plants 0.5–3.5 dm. tall, branched from the base, the branches erect or ascending, or rarely simple below, the undeveloped basal buds then forming a noticeable tomentum-covered thickening at the ground; herbage heavily white-tomentose, tomentum mostly persistent or the herbage becoming glabrate; glands entirely absent or sometimes present at the tips of inner involucral bracts; basal leaves 1.5–11.5 cm. long, obovate to oblanceolate, irregularly toothed to entire, acute; cauline leaves ovate to oblongish, entire, acute, to 2.5 cm. long, passing into the small appressed bract-like leaves of the branchlets; inflorescence cymose-paniculate, the heads generally borne singly, 13–18-flowered; involucres turbinate, 1–1.2 cm. long, the bracts somewhat squarrose, more or less woolly with dark acute tips, the inner bracts sometimes tinted with lavender; corollas palmately liguloid or tubular-funnelform, pinkish to lavender; style-branches 1.9–2.5 mm. long, appendage penicillate-subulate, 0.6–0.8 mm. long; achene 3–5 mm. long, slender-oblong; pappus bristles 40–55, in two series, unequal, up to 8 mm. long, free to the base; cotyledons obtuse to minutely obcordate, without a callous grain at apex.

Open grassland of low hills and valleys in Santa Clara and San Mateo counties and from Marin Co. north to Sonoma and east to Yolo Co., 50 to 700 ft. June–Oct.

Localities.—Hills east of Santa Rosa Valley, E. L. Greene, Sept. 15, 1888 (type, UC); Los Gatos, Santa Clara Co., Heller No. 7537 (isotype of *L. imbricata* Greene, UC, S); Searsville, five miles west of Stanford University, Baker No. 1834 (isotype of *L. bakeri* Greene, UC, Cl); Portola, San Mateo Co., Abrams No. 1004 (S, Cl); Lake Pilarcitos, San Mateo Co., Davy, June, 1893 (UC); Corte Madera, Marin Co., J. T. Howell No. 2233 (showing the effect of grass fire which occurred one month before the collection was made, H); Baltimore Park, Marin Co., J. T. Howell No. 2192 (H); San Rafael, Marin Co., Wilkes Expedition, 1841 (G; see note below); Ignacio, Marin Co., Jepson No. 9428 (J); Calistoga, Napa Co., J. T. Howell No. 2210 (H); Woodland, Yolo Co., Blankinship, Sept. 25, 1892 (UC).

The specimen of this species collected by the members of the Wilkes Expedition at San Rafael is on the type sheet of *L. ramulosa* Gray and was mistaken by Gray (1849, 1874) for that species.



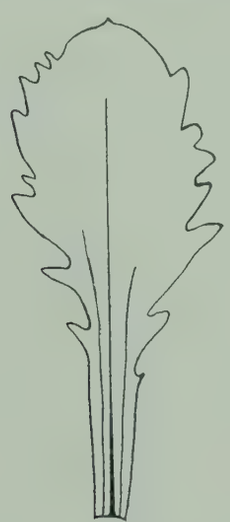
Figs. 61–67. *L. hololeuca* Greene. 61, cotyledon, from garden cultures. × 2½; 62, seedling habit, from garden cultures. × ½; 63, basal leaf, from garden cultures. × 1; 64, flower from margin of head. J. T. Howell No. 2192. × 5; 65, flower from center of head. J. T. Howell No. 2192. × 50; 66, appendage of style-branch. J. T. Howell No. 2192. × 50; 67, achene and pappus. J. T. Howell No. 2222. × 5.

a. **Lessingia hololeuca** var. **arachnoidea** (Greene) J. T. Howell n. comb.

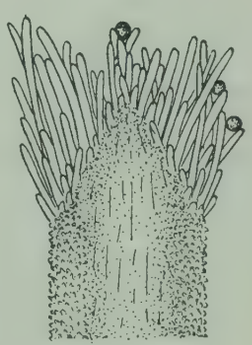
Figures 68–70

Lessingia arachnoidea Greene, Leaf. Bot. Obs., 2:29, 1910.

Plants simple from the base, widely paniculate-branched above, 3–7 dm. tall; herbage glabrate, glands absent or rarely present on



68



69



70

Figs. 68–70. *L. hololeuca* var. *arachnoidea* J. T. Howell. 68, basal leaf, from garden cultures. × 1; 69, appendage of style-branch. J. T. Howell No. 2022*A*. × 75; 70, achene and pappus. J. T. Howell No. 2022*A*. × 5.

involucral bracts; heads 8–18-flowered or the flowers as few as three; involucre 6–9 mm. high, turbinate, the bracts numerous, arachnoid-tomentose, appressed; style-branches 0.7–1.4 mm. long, appendage 0.22–0.36 mm long, with or without cusp; achene 3 mm. long; pappus reduced to a setose crown, the bristles 14–27, less than 3 mm. long, conspicuously barbellate-margined, free or becoming united into sets; cotyledons as in the species.

Hills and mountains of the outer Coast Ranges in San Mateo, Santa Clara, and Santa Cruz counties, 300 to about 2000 ft. Aug.–Oct.

Localities.—Crystal Springs Lake, San Mateo Co., Baker No. 1548 (isotype of *L. arachnoidea* Greene, UC, Cl, CA); between Lake San Andreas and Crystal Springs Lake, San Mateo Co., J. T. Howell No. 2220 (H; the plants in this collection intergrade with typical *L. hololeuca*); north end of Crystal Springs Lake, J. T. Howell No. 2220*A* (H); hills east of Los Gatos, Santa Clara Co., Heller 13529 (S); eastern slope of Loma Prieta, Santa Cruz Co., Davy, Oct. 4, 1893 (J).

BIBLIOGRAPHY

Bentham, G.
1873. Notes on the classification, history, and geographical distribution of the Compositae. Jour. Linn. Soc. Bot., **13**:335.

Chamisso, A. von
1820. Journal, *in* Otto von Kotzebue, A voyage of discovery into the South Sea and Bering's Straits . . . . 1815 to 1818, **3**:38; translated by H. E. Lloyd (London, 1821).

Gray, A.
1849. *In* G. Bentham, Plantae Hartwegianae, 314.
1874. *In* J. Torrey, Botany of the United States Exploring Expedition during the years 1838 to 1842, **17**:336.

Greene, E. L.
1896. Pittonia, **3**:58.

Hall, H. M.
1907. Compositae of Southern California, Univ. Calif. Publ. Bot., **3**:66.

Hartweg, T.
1847 and 1848. Journal, *in* Jour. Roy. Hort. Soc. London, **2**:121, 187; **3**:217.

Jepson, W. L.
1897. Erythea, **5**:35.
1925. A manual of the flowering plants of California, 11.

INDEX

Species, Varieties, and Synonyms Occurring in the Taxonomic Treatment of the Genus Lessingia

adenophora, 38.
albiflora, 29.
arachnoidea, 42.
bakeri, 40.
bicolor, 37.
cymulosa, 28.
fastigiata, 28.
germanorum, 11.
  var. glandulifera, 22.
  var. lemmonii, 25.
  var. parvula, 17.
  var. pectinata, 18.
  var. peirsonii, 26.
  var. ramulosissima, 24.
  var. tenuis, 16.
  var. tenuipes, 20.
  var. tomentosa, 24.
  var. vallicola, 19.
glandulifera, 22.
  var. *albiflora*, 29.
  var. *pectinata*, 18.
glomerata, 34.
heterochroma, 16.
hololeuca, 40.
  var. arachnoidea, 42.
imbricata, 40.
lemmonii, 25.
leptoclada, 30.
  var. *hololeuca*, 40.
  var. *microcephala*, 27.
  var. *tenuis*, 30.
  var. *typica*, 30.
mendocina, 28.
micradenia, 39.
nemaclada, 27.
  var. albiflora, 29.
  var. mendocina, 28.
nana, 35.
  var. *caulescens*, 36.
paleacea, 28.
parvula, 17.
parryi, 36.
pectinata, 18.
ramulosa, 37.
  var. adenophora, 38.
  var. micradenia, 39.
  var. *microcephala*, 27.
  var. *tenuis*, 16.
ramulosissima, 24.
subspicata, 33.
tenuis, 16.
  var. *jaredii*, 17.
tomentosa, 24.
virgata, 33.
  var. glomerata, 34.

THE ORIENTAL GENERA OF POLYPODIACEAE

BY

EDWIN BINGHAM COPELAND

"Ignoto Genere proprio
nulla descriptio, *quis accurata tradita,*
certam demonstrat,
sed plerumque fallit."

Quoted, from Caesalpinius, as the motto or text of the systematic botanist's Book of Genesis,
—Linnaeus' *Species Plantarum.*

University of California Publications in Botany
Volume 16, No. 2, pp. 45–128
Issued September 4, 1929

University of California Press
Berkeley, California

Cambridge University Press
London, England

THE ORIENTAL GENERA OF POLYPODIACEAE

BY

EDWIN BINGHAM COPELAND

The subject of the genera of ferns is a large one, and has been treated many times. The ferns themselves seem to have exerted a peculiar fascination, which drew the attention of botanists to them and to their classification, to an extent quite out of proportion to their numbers, certainly out of proportion to their practical importance.

It is not necessary to recapitulate here the various schemes of arrangement which have been proposed, and which have found more or less favor. So far as the older ones have enduring importance, this will appear as the several genera come up for discussion. Going back only as far as these schemes were animated by an ambition to present a natural classification—but noting that in this group such an effort did not by any means wait for Darwin—instead of resting merely on some feature of resemblance or difference convenient for artificial classification, the outstanding figures in this history have been:

1. C. B. Presl, professor in Prague, author of a number of papers on ferns, of which his Tentamen Pteridographiae, published in 1836, and Epimeliae Botanicae, dated 1849, are devoted particularly to the genera of ferns. Although Presl based his classification primarily on a single group of characters, those of the skeletal structures, he was careful to justify this by the plea that the resulting classification was a natural one.

2. J. Smith, curator of the great Kew Gardens. His most noteworthy publications were "An Arrangement and Definition of the Genera of Ferns, with observations on the Affinities of each Genus," read before the Linnaean Society, and published in the Journal(s) of Botany from 1841 to 1843; and Historia Filicum, 1875, a book of over 400 pages, which presents in tabular form the chief schemes of classification up to that date.

3. A. L. A. Fée, professor in Strassburg, author of a series of eleven Mémoires sur la famille des Fougères, of which the Fifth, published in or soon after 1850, is a comprehensive presentation of the genera.

4. L. Diels, as author of the sections on most of the ferns in Engler and Prantl's Natürlichen Pflanzenfamilien.

The studies of Presl, Smith, and Fée, pre-Darwinian in time but not in point of view, which had placed Pteridology for a time well in advance of sister lines of botany, were obscured presently by the shadow of Sir William Hooker, whose genera, in his later years, were at best definable groups, regardless of the affinity, or its absence, of the component species. Christ, in his Farnkräuter der Erde, undertook a return to sounder ideals. But from the neglect of scientific principles imposed by the prestige of Hooker and his school, only the rival prestige of the Berlin school was strong enough to bring an effective reaction. Diels' genera, and their arrangement, were maintained, with little change, in the Index Filicum of Carl Christensen, a work whose transcendent usefulness threatens to produce again a period of frozen sterility, like that which followed the Species Filicum of Hooker and the Synopsis Filicum of Hooker and Baker.

For a much more complete historical review of this subject, the reference to Smith's Historia Filicum may be repeated. Another excellent review, with a discussion of the principles involved, may be found in the introductory pages of Giesenhagen's Farngattung Niphobolus (1901).

A work of this kind, if worth while at all, must at least exemplify the scientific spirit of its own time. Better yet, if it can express to some extent the sounder points of view of years to come; but it must at any rate not be hampered by mental fetters already wearing out.

Systematic Botany today is dominated by two principles:

1. Its groups of plants, of generic or of whatever rank, *must* be natural, in the evolutionary sense.

2. These groups *should* be convenient—easy to recognize and to define.

Note the auxiliary verbs; the second principle can never again take precedence over the first. If, by convergent evolution, which in some instances surely occurs, there arise two similar groups of unlike ancestry, they *must* be recognized as distinct, whether it be as species, or as genera, or whatever the rank of the groups, and however difficult it may eventually become to distinguish them by definition.

For example: *Polypodium* and *Davallia* are genera not nearly related, and, typically, easily distinguished by eye and by definition. One, or two, or three groups of the descendants of *Polypodium* follow

such lines of evolution that the resulting ferns, though their real affinity is in these instances clear to the experienced eye, have seemed to conform to the brief customary definition of *Davallia.* Blume, a century ago, and before him Sprengel, called them *Davallia,* in harmony with the scientific views of their time. Hooker did the same, violating his own principles as an illustrious evolutionist. And Christensen, as late as 1913, makes new names for at least seven of these ferns, justifying the fear already expressed, that the prestige he has earned by facilitating and insuring the accuracy of our library work will be used to impair the freedom of our brains.

The principle of naturalness bars these ferns from *Davallia.* The principle of convenience decides what shall be done with them, and offers us two alternatives. We may, since they are descendants of *Polypodium,* place or retain them in that genus. This is the course adopted by Hayata[1] and Brause.[2] If this suits their ideas of convenience, their course is proper, but it does not suit mine. If either author, in the publications cited, had felt called upon to define his genus *Polypodium,* he might have found a reason for recognizing *Prosaptia* and *Acrosorus* as genera.

If, on the other hand, these authors (using them as examples because their work is recent and because the case of these ferns is an exceptionally clear one) felt that the manifest and completely understood descent of these ferns from *Polypodium* made their inclusion in that genus compulsory, regardless of convenience, then their position is hardly more tenable than Christensen's. Such a view makes every group of plants we try to recognize—species, genus, and family alike—a mere token of our ignorance. But this is not what they really are. However arbitrary the limits we put upon them, they still exist as natural entities. We recognize any branch of a tree and, after we see whence it springs and what minor branches and twigs it bears in turn, we know it better than before. If, sometime, we understand the tree of life completely, in all its parts, surviving and extinct, and understand in all the detail of their evolution the relation of each twig to every other, we will not therefore reduce all plants to a single kind; but will still distinguish the finer twigs as species, the branchlets as our genera, and the greater branches, with their divisions and twigs, as our groups of higher order.

---

[1] Icones Plant. Formos., 5:326, 1915, as to *Prosaptia.*

[2] Engler's Jahrb., 56:183, 1912, as to *Acrosorus.*

When I understand with some confidence the origin of a genus, I am not constrained to reduce it to its parent. It is only then that I get real confidence in its generic status.

As a minor consideration, size of group is a factor in determining its convenience. The genus is intermediate between the species, a single "kind" of plant, and the family. The genus must be natural and should be convenient, in size as well as otherwise. If genera were almost as numerous as species, or almost as large as families, we would have little object in giving them a place in our scheme of classification. Other things being equal, we are therefore indisposed to break little genera up into smaller ones, but may be glad to break up very large genera. *"Pleurogramme"* is so small a genus that one would not divide it unless compelled so to do by clear evidence that it is polyphyletic. *Vittaria, Cyclophorus,* and *Lindsaya,* though not small genera, are not yet inconveniently large; occasion for dividing them seems to have been found, but there is no real object in this if they are already monophyletic. On the other hand, if *Phegopteris* and *Alsophila* were natural groups we would gladly hold them separate from *Dryopteris* and *Cyathea,* because these genera are inconveniently large. But convenience will not justify us in dividing a genus of a thousand species along any except natural lines; nor let us maintain a genus of two species, unless they are nearly related.

While the first principle stated above—that a genus must be natural—is accepted today as almost axiomatic, we are not yet so used to being bound by it that lapses are not still common. Deference to it makes it impossible to maintain the family Polypodiaceae, with the limits and definition accepted for some time past; including all ferns with a longitudinal annulus interrupted by the stalk of the sporangium, and practically only these. The ferns comprising a family so defined are not one phyletic group, and cannot therefore compose a proper family.

At least three great groups of genera regarded as polypodiaceous are independently descended from ferns with the annulus oblique. Under our principles, we have two alternatives:

1. We can make the family homogeneous by including in it more primitive ferns, going back as far as independent origin has become apparent. In practice, this is probably accomplished if we include Cyatheaceae and Matoniaceae, in the sense of Engler and Prantl and of Christensen.

2. We can raise the several phylogenetic series to family rank.

Neither of these courses is free from objection. If we adopt the first, we get a very large and internally diversified family. And it may next become apparent that we have not yet gone far enough down toward the primitive Pteridophytes to achieve real homogeneity. If we adopt the second alternative, there is no evident limit to the number of families which will result. If we assume, or anticipate, for a moment that the three great groups of genera can be traced back approximately to *Cyathea, Dicksonia,* and *Matonia,* then at least these three groups will become families. Nobody can come near to defining any one of the three in words. To make the families definable, their number is increased. First, the bottom of each series is cut off, and we recover Cyatheaceae, Dicksoniaceae, and Matoniaceae. The next internodes of the tree follow in quick succession; Plagiogyriaceae, Dennstaedtiaceae, Dipteridaceae, and Cheiropleuriaceae are already proposed. We will have back the old Davalliaceae, Aspleniaceae, Vittariaceae, etc., *ad infinitum.*

This would be bad enough if the taxonomic dissection could be restrained to the application of probable knowledge; but it will result also from avowed ignorance. In what series will *Asplenium* fall? *Woodwardia, Nephrolepis, Oleandra, Neurosoria, Lomagramma?* We cannot anticipate otherwise than that doubt, as well as understanding, will result in the proposal of family after family, probably a score of them within a decade. And still they will be undefinable. *Athyrium* will be just as open to confusion with *Dryopteris,* in one direction, and with *Asplenium,* in another, whatever the taxonomic rank of these groups; and the higher this rank is made, the greater will be the resulting practical difficulty. The first alternative, the recognition of one comprehensive family, is clearly the preferable one.

This argument is presented at some length, because the issue has become a very live one. It is more than twenty years since the polyphyletic character of Polypodiaceae, in the then accepted sense, became clear to me. It is a decade since I tried to forestall the multiplication of families.[3] Now, the many small families are being proposed.[4] Bower's procedure follows one of the two scientifically possible courses. If it had been possible for this course to lead only as far as Plagiogyriaceae, I would have welcomed it, but it does not and cannot. It is hard for me to believe that he would have begun the proposal of new families if he had undertaken to locate all of the genera before publication began.

[3] Sarawak Museum Journal, 2:292 *et seq.,* 1917.

[4] F. O. Bower, The Ferns, vol. 2, pp. 252, 275, 282, etc.; but not vol. 3.

The purpose of this paper is two-fold. Primarily, it is to present an attempt to classify the genera in a manner more natural than has been presented before. Secondarily, it is an elaboration of the plea just made, for the conservation of Polypodiaceae as one family, however great it may have to be to be a phylogenetic unit. I do not undertake to define most of the genera except by their affinities; nor to justify the names used for all of them; nor even to mention synonyms, except when a question of phylogeny is involved. To do these things well would require a large book, and would distract attention from my thesis. Neither would it be worth while, in a treatise on the ferns of only a part of the world.

Geographical limitation is clearly open to objection in the case of phylogenetic discussion; and it operates especially to weaken my treatment of the group called Pterideae in recent works. My apology is that I try to do what I can. It is not by "knowing" a fern in each genus, or the diagnostic characters of the genera, that one acquires an understanding of their affinities. Such acquaintance may do very well with such genera as *Ophioglossum, Marsilea, Lygodium,* etc., which however large are isolated. It is merely a degree of ignorance, in cases like *Athyrium, Dryopteris,* and *"Polypodium."* It is long and intimate acquaintance with very many of the species, with a steady interest in their relationships, which reveals these affinities, now here, now there, often suggested by peculiarities previously deemed unworthy of serious attention. It is because I have a measure of such knowledge of Oriental ferns, that I undertake to improve their classification; it is because I have no such familiarity with American ferns that I cannot discuss their evolution here.

That this classification is more natural than any of its predecessors is in the nature of the case. It is about thirty years since the last attempts at classification of these genera as a whole, by Diels and by Christ; and our knowledge has expanded very much in the interim. I do not anticipate that the arrangement proposed here will prove as durable as Diels's. To the extent that I may draw attention to the internal phyla of the Polypodiaceae, further improvement of their classification will be invited and stimulated. To facilitate change, I have adopted a system of numbering, familiar in family genealogies and in library catalogues, but, so far as I know, altogether new in botanical classification. The internally independent lines of evolution bear their several unit numbers, 1, 2, 3, etc., as many as the recognized lines. These first figures of the number indicate the main branches of

Acc No: -5539

the tree, the most remote ancestor considered in the genealogy. The supposed first divisions of this branch, like the next to the most remote ancestor, are shown by the second figure, and so forth.

This arrangement is altogether plastic, subject to modification with every improvement of knowledge. When fresh understanding shows that the place of a genus should be changed, no vacancy is left in its previous place, and there is always room for it in its new one. For example, my herbarium was arranged and numbered in the belief that Davallieae—the genus *Davallia* of Hooker and Baker (excluding *Prosaptia*)—was a natural group. The genus *Davallia,* in the narrower present sense, was then numbered 241131, indicating descent through the line *Dicksonia-Dennstaedtia-Microlepia.* I have since become satisfied that such is not the line of its descent; that, except possibly *Dicksonia,* these genera are on a divergent evolutionary branch; and that *Oleandra* is closer to its line of descent than is any other existing genus. Nothing need be easier than to make the appropriate change in number and place. So far as I now recognize the uncertainties of my arrangement, there is only one genus or group of genera which may eventually require a considerable change of position, and is of such size that this would be difficult in the herbarium; this is *Asplenium,* with its daughter genera.

The day is past, by a full half-century, when justification for an attempt like this is reasonably demanded. It comes like an echo from the tomb when we read in these times that "the tracking of . . . . descent, which depends as a rule on not to be proved suppositions or personal conceptions, is too trifling and the mention of it too worthless to take into consideration for systematic-botanical publications." It is with an interest in variety, uncontaminated by any effort to interpret, that children collect tobacco tags. It is by its distinctive effort to interpret that systematic botany maintains the dignity of a science and recovers the place in the university curriculum which it almost lost for a period. A general discussion of the kinds of evidence, and of its validity, would not be so uncalled-for as justification of the task; but I abstain from this, partly because it would merely weary those already saturated with the idea, partly because the eventual discussion of individual genera may serve the same purpose well enough.

ENUMERATIO GENERUM

10 Plagiogyria
120 Cyathea
1211 Matteuccia
1212 Onoclea
1221 Diacalpe
1222 Peranema
1223 Monachosorum
1224 Acrophorus
1225 Stenolepia
1231 Cystopteris
1232 Woodsia
1233 Ptilopteris

124 Dryopteris
12401 Currania
12402 Psomiocarpa
12403 Heterogonium
124031 Stenosemia
12411 Haplodictyum
12412 Sphaerostephanos
12413 Dictyocline
1242 Polystichum
12421 Cyrtomium
12422 Egenolfia
12431 Cyclopeltis
12432 Didymochlaena
1244 Tectaria
12441 Tectaridium
12442 Hemigramma
12444 Quercifilix
12445 Cionidium
12446 Luerssenia

125 Athyrium
12521 Blechnum
12522 Doodia
12523 Brainea
12524 Woodwardia
12525 Sadleria
1253 Asplenium
125311 Ceterac
125312 Pleurosorus
12532 Camptosorus
125331 Phyllitis
125332 Diplora
125333 Boniniella
12534 Diellia
12535 Stenochlaena
12536 Lomagramma
12537 Thysanosoria

20 Dicksonia
21 Cibotium
22 Cystodium
2211 Nephrolepis
230 Orthiopteris
231 Ithycaulon
24 Balantium
241 Dennstaedtia
2411 Microlepia
24111 Oenotrichia
24120 Tapeinidium
24121 Sphenomeris
24122 Protolindsaya
24123 Lindsaya
24130 Schizoloma
24131 Taenitis
24132 Syngramma
24133 Craspedodictyum
24134 Hemionitis
24135 Gymnopteris
24136 Aspleniopsis
2413x Pityrogramma
2413x Anogramme

2420 Leptolepia
2421 Hypolepis
24211 Paesia
24212 Pteridium
24213 Histiopteris
24214 Pteris
242141 Coniogramme
242142 Acrostichum
24215 Schizostege
24221 Cheilanthes
24222 Notholaena
24223 Pellaea
24224 Doryopteris
24225 Onychium
24226 Cryptogramma
24227 Actiniopteris
2422x Neurosoria
243 Adiantum

30 Oleandra
31 Araiostegia
32 Davallodes
321 Trogostolon
322 Leucostegia
323 Humata
324 Davallia
325 Scyphularia
3x Arthropteris

40 Matonia
401 Phanerosorus
41 Dipteris
4211 Christiopteris
4212 Cheiropleuria
4213 Hymenolepis
4221 Platycerium
4222 Cyclophorus
4223 Drymoglossum
4224 Elaphoglossum

423 Polypodium
4231 Prosaptia
4232 Grammitis
42321 Oreogrammitis
42322 Cochlidium
42323 Calymmodon
42324 Acrosorus
42325 Loxogramme (Paltonium)
424 Goniophlebium

425 Microsorium
4251 Diblemma
4252 Leptochilus
4253 Dictymia
4254 Selliguea
42541 Campium
4255 Dendroconche
4256 Aglaomorpha
42561 Drynaria
42562 Thayeria
42563 Merinthosorus
42564 Photinopteris
4257 Lecanopteris
426 Phlebodium

51 Antrophyum
52 Vittaria
53 Vaginularia
54 Monogramma

10. **Plagiogyria** Mett., Abhandl. Senckenb. Naturf. Ges., 2:265, 1858.

The type species as described was *Plagiogyria biserrata* Mett., *ibid.*, p. 272. The type specimen is in the herbarium of the Berlin Botanic Garden. By general agreement, this is identical with *P. semicordata* (Presl) Christ, *Lomaria semicordata* Presl, Epim. (1849), 155; but the generic type is still properly the type specimen of Mettenius.

The systematic place of *Plagiogyria* has been so thoroughly discussed by Bower, Ferns, II (1926), 275, and in my own recent monograph of the genus (Phil. Jour. Sci., April, 1929), that no further comment is needed here.

Though the absence of paleae, the oblique annulus, and the approximately simultaneous maturity of most of the sporangia suggest that this genus is primitive in character, as compared with the great body of the Polypodiaceae, it has not the diversification of species nor the geographical distribution of an ancient fern. Neither do the local diversity and number of species in its home area (China, Borneo) let it be regarded as a group merely enduring from a remote past. Rather than either of these, it affords a demonstration that evolution is still active among ferns of somewhat primitive type, as well as among those most characteristically recent.

I have recognized thirty-two species: twenty-three in the Orient, with a center of distribution in China, and with species ranging to India, Java, Celebes, and Japan; and nine in the American tropics.

12. **Cyathea** Smith, Mém. Acad. Roy. Sci., Turin, 5:416, 1793.

The first species listed are *Cyathea horrida* and *C. multiflora.* As the first of these is decidedly aberrant, and the second is far from typical, and as both have been separated from *Cyathea* in the past by most writers, and the renaming of the great group would be a nomenclaturial catastrophe, we will do well to agree upon *C. arborea,* the third of Smith's species, as the standard species of the genus. Its type is *Polypodium arboreum* L., in the herbarium of the Linnaean Society in London.

As here construed, *Cyathea* includes more than six hundred recognized species, very numerous in both hemispheres but with comparatively few in Africa and India. When its groups are better known as such than they are now, it may well be advisable to break up a genus of such size into smaller natural genera. *Amphidesmium* (rather than *Metaxya*) and *Lophosoria* are such genera (see Bower, Ferns, II, 282), not treated here because confined to America.

Alsophila and *Hemitelia,* as commonly construed, are not genera in any modern scientific sense. *Alsophila* is a catch-all for species without an indusium and specimens so collected; *Hemitelia,* for those with the indusium incomplete. But the tree ferns are not divisible, naturally, into any two or three or more groups with indusial characters. We might try to recognize a real genus *Alsophila,* with a dozen or so of species. But the great majority of exindusiate species are scattered through a considerable number of natural groups, or compose such groups, each evidently related to indusiate species. One of the most distinct of such groups is *Gymnosphaera* Blume, in which if I were dissecting *Cyathea,* I would include *Thysanobotyra* v.A. v.R.

1211. **Matteuccia** Todaro, Syn. Pl. Acot. Vasc. Sicil. (1866), 30.

The type species is *Osmunda Struthiopteris* L. The type is in the herbarium of the Linnaean Society, London.

Osmunda Struthiopteris L. occurs well throughout the north temperate zone, excepting western North America. The only other known species are *M. orientalis* (Hooker) Trev., from the Himalayas to Japan, and *M. cavaleriana* (Christ) C. Chr., in China.

Christ, Hedw. 47:150, 1907, regards this genus as an aberrant *Dryopteris.*

1212. **Onoclea** Linnaeus, Spec. Pl. (1753), 1062.

The type and only recognized species is *Onoclea sensibilis* L., *ibid.* The type specimen is in the herbarium of the Linnaean Society, London, received by Linnaeus from Virginia. It is common in eastern North America and temperate eastern Asia, being one of a considerable number of plants which, by this present distribution, testify to their circumpolar distribution in preglacial time.

Christ regards this as nearly related to *Tectaria*, this being suggested by the venation. My own view, following general past opinion, is that *Onoclea* and *Matteuccia* are much nearer to one another than either is to any other fern.

1221. **Diacalpe** Blume, Enumeratio (1828), 241.

The type species, the only one recognized, is *Diacalpe aspidioides* Blume. The type specimen is in the herbarium of the University of Leyden.

Java to Luzon, China and India; not found in the southern Philippines, and in Borneo only on Mount Kinabalu.

Blume remarked on the resemblance to *Woodsia* and to *Aspidium* (*Dryopteris*), when describing the genus.

1222. **Peranema** Don, Prod. Fl. Nepol. (1825), 12.

The type species is *Peranema cyatheoides* Don, *ibid.* Don cites no specimen or collector. His herbarium is in that of the British Museum.

P. cyatheoides is known in the north and south of India. *P. formosana* Hayata is not very different. *P. luzonica* Copel. is much more scaly and coriaceous. No other species is known.

Don's observation, following the diagnosis, is "Genus a Cyathea, cui affine, omnino distinctum: indusiis sphaericis indivisis pedicellatis." The stalked sori mark it very clearly.

1223. **Monachosorum** Kunze, Bot. Zeit., 6:119, 1848.

The type species is described as *Monachosorum davallioides*, a synonym of *M. subdigitatum* (Bl.) Kuhn. The type specimen, from Java, is probably in Leyden.

The range is from Malaya to India and Formosa. *M. Henryi* Christ, described from Yunnan, is very similar.

1224. **Acrophorus** Presl, Tent. Pterid. (1836), 93.

The type species, as cited by Presl, is *Acrophorus nodosus* (Blume) Presl, *Aspidium nodosum* Blume Enum. (1828), 171. The type

specimen is in the Rijksherbarium in Leyden. Blume's name was invalid, and the species is now known as *A. stipellatus* (Wall.) Moore.

The range is from Java and New Guinea to Formosa and northern India. Of this group of five genera, *Acrophorus* is the only one extending east to New Guinea.

1225. **Stenolepia** v.A. v.R., Bull. Dept. Agr. Ind. Néerl., 27:45, 1909.

The type and only species is *Stenolepia tristis* (Blume) v.A. v.R., *Aspidium triste* Blume, Enum. (1828), 169, known only on Alpine summits in Java.

The preceding five genera constitute a very natural group, characterized as a whole by stout, erect caudices; many large paleae; ample, much dissected, deltoid fronds with opposite pinnae, commonly attached to enlarged "nodes" of the rachis, and definite sori. The indusia are various or none. All inhabit the same small geographic area and are characteristically ferns of the high mountains. They evidently are not more related to *Woodsia* than to *Dryopteris,* to some species of which there is a rather close resemblance.

1231. **Cystopteris** Bernhardi, Schrad. Neues Jour., 1^2:26, 1806.

Some recent authors prefer *Filix* Adanson (1763) as the name of this genus, but I would exclude it if only on grounds of general propriety, more fundamental than any formal rules. At least from the time of the recognition of *Filices* Tournefort, as the name of a group of plants, the singular of that name became unavailable as the distinctive name of a genus of those plants. For like reasons, nobody proposes a genus *Planta,* or *Arbor,* or *Herba.*

The type species is *Cystopteris fragilis* (L.) Bernh., *Polypodium fragile* L. The type specimen is in the herbarium of the Linnaean Society, London. This species occurs well over the northern hemisphere and beyond the equator. It is very nearly related to those groups of *Dryopteris* and *Athyrium* which can hardly be distinguished from one another. These groups have no established and dependable indusial characters, and *C. fragilis* would not be a very foreign element in either of them; if reduced to either, it would better be to *Athyrium.* It is by no means so near to *Acrophorus,* which has an indusium of the same appearance.

Indusial evidence has been unduly relied upon in assigning species to *Cystopteris. C. Douglasii,* of Hawaii, is rather an *Athyrium. C. japonica* might probably better be called *Dryopteris.* Brause, Engl. Jahrb., 56:78, 1920, states that *C. setosa* Bedd. is identical with

C. tenuisecta (Blume) Mett.; but its affinity to *Dryopteris vilis* (Kze.) O.K. is much closer than to *C. fragilis.* Incidentally, *Hypolepis tenerifrons* Christ is a member of the same group of species. The two supposed species of *Cystopteris* in New Zealand are unknown to me; Cheesman, Manual (1906), 957, reduced them to *C. fragilis.*

1232. **Woodsia** R. Br., Prod. Fl. Nov. Holl. (1810), 158.

The type species is *Woodsia ilvensis* (L.) R. Br., *Acrostichum ilvense* L. The type specimen is in the herbarium of the Linnaean Society, London.

Two or three dozen species are assigned to this genus. They are world-wide in occurrence, the chief center being in China. It is not a uniform group and will eventually be broken up into several. The type species is probably related to *Cystopteris.* Some others—*W. polystichoides,* and some of very different aspect—strongly suggest *Polystichum.* In another direction, Linnaeus may have been right in describing the resemblance to *Notholaena* as a strong affinity.

1233. **Ptilopteris** Hance, Jour. Bot., 22:138, 1884.

We have here a condition quite unusual at so late a date. Hance described his new genus and stated that it contained two species known to him—*Ptilopteris Hancockii* n. sp., there described, and *Pt. Maximowiczii* (Baker), *Polypodium Maximowiczii* Baker. His generic diagnosis is perfectly applicable to *Pt. Maximowiczii,* but his *Pt. Hancockii* is a *Polystichum.* Baker redescribed it, from the same collection, as *Polyst. reductum;* Hance's specific description seems to apply to a *Polystichum;* and Professor Gepp has been kind enough to consult Hance's type, in the British Museum, and writes that it is clearly not congeneric with *Pt. Maximowiczii.* Since Hance set up a genus fitting *Pt. Maximowiczii,* and not *P. Hancockii,* and since *Pt. Maximowiczii* is not properly a member of any older genus, the reasonable course seems to be to recognize this as the *standard species* of the genus. There is a second Japanese species; and a doubtful third species in Yunnan.

Its origin is very probably in or near *Cystopteris,* whether or not through *Woodsia*—cf. Christ, Hedwigia, 47:151, 1908. It is not related to *Polypodium,* where first described, nor very closely to *Polystichum,* nor to *Monachosorum,* to both of which it has been referred.

124. **Dryopteris** Adanson, Fam. des Plantes, 2:20, 1763.

The accepted type is *Dryopterus Filix-Mas* (L.) Schott., which in various forms is effectively cosmopolitan.

There has been much dissatisfaction because of the rehabilitation of this generic name, but no practicable alternative would have been more satisfactory.[4a]

As construed by Christensen in his Index, this genus probably contains fully a thousand distinct described species, most abundant in Malaya and tropical America, but common everywhere. With very few exceptions, they are terrestrial ferns, with rhizomes erect or prostrate but rarely long. It includes a considerable number of natural groups which it will be convenient to recognize as genera. But these are not the groups, defined by indusial characters alone, treated as genera in the standard works of a half-century ago; nor even, in general, these groups as further divided solely according to peculiarities of venation. The discrimination of the natural groups among the American species has already been undertaken by Christensen, and these are evidently largely the same in Malaya, showing that as a whole they are really old. In the hope that Christensen will himself apply his studies to the group in the Old World, I abstain here from the recognition as genera of our larger groups of *Dryopteris* species.

Among these groups, the most primitive may be judged on a number of grounds to be one with ample, compound fronds, short or erect rhizomes, free veins, with broad paleae on the rhizome and the bases of the stipes but without characteristic hairs. Its sori are dorsal, on the lamina and on the veins, round, and provided with a roundish indusium fixed by the middle of its side. There is no dependable distinction between these most primitive *Dryopteris* species and those at the bottom of the *Athyrium* series. As the groups differentiated, the *Dryopteris* sorus remained round and the point of attachment became the top of a sinus, while the *Athyrium* sorus elongated along the vein, with a line, instead of a point, of attachment. The genera merge so completely at the bottom, that the assignment of species to one or the other is better done on the basis of any characters which happen to indicate affinity to definitely placed

[4a] This was written before the publication of "Schmiedel's Publication of Thelypteris" by Fernald and Weatherby, Rhodora 31 (1929), 21, and is not intended to express judgment as between *Dryopteris* and *Thelypteris*. I would like a "court decision"—action by a botanical congress—before taking up *Thelypteris* as a genus. If its use be thus sanctioned, however, the resulting complication of synonymy should not be serious. The natural dissection of the larger group here and in the Index Filicum called *Dryopteris* will leave *Dryopteris sensu strictiore* and *Thelypteris*, properly typified, as distinct genera.

species, than on the basis of the characters of the sorus alone. The near affinity of *Cystopteris* to these primitive species has already been noted.

The two large genera, *Tectaria* (or *Aspidium*) and *Polystichum,* clearly are more nearly related to *Dryopteris* than to *Athyrium.* Assuming that *Dryopteris* and *Athyrium* are literally twin genera—a condition unusually clear in this instance—we are forced to the conclusion that *Tectaria* and *Polystichum* are descendents of *Dryopteris;* the usual alternative—that they have a source in common with it but farther back—being excluded in this case. This establishes *Dryopteris* as the parent genus of any "tribe" which properly can retain the name, well established in literature, of *Aspidieae.* Besides the two large genera named, and such others as may be segregated from the present *Dryopteris,* there are several small ones in each hemisphere evidently derived from *Dryopteris.*

12401. **Currania** Copeland, Phil. Jour. Sci., 4*c*:112, 1909.

A small genus of Phegopterid ferns, found in China, Japan, and the Philippines. The type species is *Currania gracilipes,* of which the type is in the herbarium of the Bureau of Science, Manila. The fronds are glabrous, deeply pinnatifid, with the lowest segments somewhat deflexed and sometimes slightly enlarged, the frond bent at its insertion on the slender, erect stipe, so that it usually slopes down from that point. The sori are naked and elongate. The genus can be reduced to synonymy, in *Dryopteris,* but will still constitute a quite distinct group if this is done; for the affinity to *D. Phegopteris* is more evident than close. If it is kept distinct, a third species, described as *Polypodium gymnogrammoides* Baker, should be added to the two already named in *Currania.*

12402. **Psomiocarpa** Presl, Epimeliae Bot. (1849), 161.

The type should be Presl's specimen of *Psomiocarpa appendiculata,* in Prag, though the specific name was proposed by J. Smith, and validated by Kunze. It is a common fern from northern Luzon to Mindanao, but unknown outside the Philippines. American species have been referred to this genus by Presl and by recent writers, but I do not believe this correct.

The affinity to *Dryopteris* is very apparent; but there is no intergrading with any species of the parent genus such as is known in *Hemigramma. D. dubia* Copel. is probably as near to this as is any

known *Dryopteris* species; but it is not unlikely that the origin of *Psomiocarpa* will be fixed more definitely in the future.

12411. **Haplodictyum** Presl, Epim. (1849), 50.

The type is the specimen of Cuming No. 322 in the Presl Herbarium at Prag. Two or three species can be distinguished, all in the Philippines.

The genus is an offshoot from the group of *Dryopteris canescens* (Bl.) C. Chr., and more specifically from *D. Bakeri* (Harr.) Copel. This connection is so intimate that the sole ground for the recognition of the genus is convenience. The elements of the generic definitions which are most conveniently used in a key to the genera are common to *Haplodictyum* and to section *Pleocnemia* of *Tectaria*. The effect is that one not knowing these ferns is likely to look for them in *Tectaria,* and that their inclusion in *Dryopteris,* the only larger genus in which they can properly be placed, involves a particular modification of the diagnosis of that genus.

For similar reasons, *Leptogramma* and *Stegnogramma* are likewise to be treated as genera; I abstain here only in order to leave the field clear for a comprehensive treatment of *Dryopteris.* The case of *Meniscium* is more complicated, because the ferns referable to it by definition are not monophyletic. This may be true also of both of the other genera just mentioned; *Haplodictyum* is introduced here chiefly as a basis of discussion. Even the convenience of treating it as a genus may not be a sufficient justification for so doing; for its diagnostic features are not very firmly established.

12412. **Spharostephanos** J. Smith, *in* Hooker and Bauer, Genera Fil. (1839), 21.

The type species is *Sphaerostephanos asplenioides,* the type of which should be in the Kew Herbarium. It is regarded as a synonym of *Aspidium polycarpon* Blume, Enum. (1828), 156, the correct name being **Sphaerostephanos polycarpa** (Blume). Its range is Malaya, north to the Peninsula and east to Polynesia. Another more striking species is local in Borneo.

The genus is so close to *Dryopteris* that its separation is only a matter of convenience. The distinctions are elongations of sorus and indusium, and the presence of copious golden glands, particularly along the margin of the indusium.

This genus has been called *Mesochlaena* R. Br. in Horsfield, Plant. Jav. Rar. (1838), 5; but *Mesochlaena* as of that date is a mere name,

without description or mention of a species. Smith later, Jour. Bot., 3:18, 1840, accepted Brown's name, cited several species (of which the only authentic one is the type of *Sphaerostephanos*), and presented a passable diagnosis; but the retraction of his name, the first published, was as impossible for Smith as for anybody else.

12413. **Dictyocline** Moore, Gard. Chron. (1855), 854, Syn. Fil. (1857), LIX.

The type is *Dictyocline Griffithii*, described from Assam. A second species, *D. Wilfordi* (Hooker) J. Sm., was described from Formosa, distinguishable by pinnate instead of pinnatifid fronds. This distinction does not hold good by itself, but it is my impression that there are two species, both occurring in Fukien. They are construed as one by Diels and Christensen, and transferred to *Aspidium*.

Dictyocline is not Tectarid but directly Dryopterid. It is very nearly related to *Dryopteris Stegnogramma* and thus to other of the Oriental species sometimes called *Meniscium*. The very characteristic hairiness, the combination of identical hairs and scales on the stipe, and the venation, along with the elongation of the sori, are evidences of this close affinity. The pinnatifid apex of *Stegnogramma* exhibits a venation pattern essentially identical with that of *Dictyocline*. Incidentally, *Stegnogramma* could receive generic recognition with at least as much reason as *Haplodictyum;* and there would be no violation of principles in then making it include *Dictyocline*.

12415. **Heterogonium** Presl, Epimeliae Bot. (1849), 142.

The type is *Heterogonium aspidioides* Presl. The type collection was presumably Cuming No. 321, but Presl cited no number. This has been confused with *Digrammaria ambigua* Presl, but I know no reason to suspect that that genus was, or included, anything except the common *Athyrium esculentum*. *Heterogonium* has an erect caudex clothed with broad, dark paleae. The fronds are moderately dimorphic, pinnate with pinnately lobed pinnae, the basal ones neither much enlarged nor forked. The venation is typically Pleocnemioid, without areolae except along the costae, and without included free veinlets. *Aspidium profereoides* Christ, Phil. Jour. Sci., 2C:158, 1907, which I once reduced to synonymy but would now restore as **Heterogonium profereoides**, has more ample fronds, with secondary areolae enclosed by veinlets excurrent from those enclosing the costal areolae. The sori are naked, and elongate when well developed; they

are arranged regularly in *H. aspidioides,* but more irregularly and with less definition in *H. profereoides.*

Heterogonium has been construed by all recent writers as *Tectaria* (*Aspidium*). The generic characters are insufficient in themselves to prevent this, the venation being like enough to that of *Tectaria* § *Pleocnemia,* and the indefinite sori being duplicated in a number of *Tectaria* species of diverse affinity. But there is no *Tectaria* known to me to which it seems nearly as closely related as it does to *Dryopteris sagenioides.* Aside from marked similarity in aspect, dissection, etc., that species, known in Java, Sumatra, and Borneo, has its upper surface hirsute, with hairs not very unlike those of *Heterogonium.* I am not sure that *D. sagenioides* is really a *Dryopteris,* but abstain, at least for the present, from attempting to show that any fern with wholly free veins is Tectarid.

124151. **Stenosemia** Presl, Tent. Pterid. (1836), 237.

The type species is *Stenosemia aurita* (Sw.) Presl, *Acrostichum auritum* Swartz, which is common in Malaya and reported from the Solomon Islands. One other species, *S. pinnata,* is not very sharply distinct, but is of interest because it stands, in form of frond, in the gap between *S. aurita* and the more primitive *Heterogonium.* In their typical development, the fertile frond of *Stenosemia* is contracted to linear segments, and the sporangia occupy their entire nether surface. But the sporangia always appear first on the veins; and what may be regarded as atavistic specimens are common, having the lamina incompletely reduced and the sporangia restricted to the veins, or even to indefinite sori partly occupying the veins. The affinity to *Heterogonium* is perfectly clear; sterile plants may not be distinguishable, and J. Smith was never able to correct his first impression, that they were specifically identical. Construing *Heterogonium* as probably Dryopterid, I dispose of *Stenosemia* in the same manner; but it is very suggestive of *Tectaria* in form of frond, and *Tectaria* is more subject to the evolution of acrostichoid offshoots than is *Dryopteris.* The similarity of the ferns here treated as related, though separated generically for the sake of convenient definition, is attested by their previous treatment. Mettenius combined two in one species, *Phegopteris philippinensis.* Christensen construed one of these as *Aspidium ambiguum* and the other as a variety of *Dryopteris sagenioides,* and the latter is said to be the one which J. Smith construed as *Stenosemia aurita.*

1242. **Polystichum** Roth, Tent. Fl. Germ., 3:69, 1800. (This was apparently published a year earlier.)

The first species listed was *Polystichum Lonchitis,* but the commonly accepted type is the fifth, *P. aculeatum, Polypodium aculeatum* L., which, as a species or large group of hardly distinguishable species, is world-wide in distribution. The number of known valid species may be one hundred and fifty, or twice that many, according to one's judgment of what are distinguishable.

The most primitive element in the genus is quite certainly that with broad, very compound fronds, represented in the Orient by *P. aristatum* and *P. carvifolium*[5] and many less widespread species, which is confusingly close to the large group of *Dryopteris* species represented, for example, by *D. spinulosa.* It may be remarked here that the argument, presented under *Dryopteris,* by which it was concluded that *Polystichum* is derived from that genus, rests on the assumptions that *Dryopteris,* as here treated, is monophyletic, and that its most primitive element is that closest to *Athyrium;* neither of these assumptions is self-evident.

As a whole, *Polystichum* is distinguishable from *Dryopteris* by its harsh fronds; coarse, dark paleae; round, peltate indusia; and the acroscopic development of the base of the divisions of the frond. The harshness appears in both texture and toothing. The more general features of aspect and texture characterize the genus better than does the indusium, which may be entirely wanting. Within the genus, as in *Dryopteris* and *Athyrium,* there has been an evolution of old and large groups of species with less divided fronds. In *Polystichum* this evolution has progressed through the group of *P. aculeatum,* containing the taxonomic type of the genus, to that with simply pinnate fronds, the group of *P. auriculatum,* exceedingly rich in oriental species. As in the great related genera, the consolidation of the fronds tends to result in reticulate venation, at which point convenience recommends the recognition of derived genera—*Cyrtomium* in the Orient and *Phanerophlebia* in America. It is likewise in general convenient to grant generic distinctness to the evolutionary lines leading to Acrostichoid fructification, and *Egenolfia* is held to represent this step in the Orient. Generic distinction of species which have lost the indusium would not result in convenience, because these species are not a monophyletic group.

---

[5] Christensen, Vid. Skrifter, 8:101, 1920. Hawaiian Ferns, 24, calls this a *Dryopteris.*

12421. **Cyrtomium** Presl, Tent. Peterid. (1836), 86.

The type species is *Cyrtomium falcatum* Presl, *Polypodium falcatum* L. fil., which, broadly construed, is found from Hawaii across Asia to Madagascar. There are several distinct enough local species in the Orient. The Hawaiian fern, *C. Boydiae* (Eaton) Rob., is positively not one of this group, however similar some of its forms may be in venation and indusium; it is an unstable *Dryopteris,* hardly a good species, though some of its forms might be treated as a derived genus if they were well established.

12422. **Egenolfia** Schott, Genera Fil. (1834), pl. 16.

The type species is *Egenolfia hamiltoniana* Schott, based on Wall. Cat. No. 29, from Sylhet, a form or species with bipinnate fertile frond. It remains customary to follow Hooker's judgment and treat all of the ferns of this genus as a single species, *E. appendiculata* (Willd.) J. Smith. In fact, the usual treatment is to then submerge the genus in *Polybotrya,* an American genus, with which any immediate affinity is more than doubtful.

The range of the genus is from India to Java, the Philippines and Formosa. At least some of the species are unstable. But it is unreasonable that, for this reason, the distinguishable species should all be reduced to one. Fée named ten of them. I do not know how many may be known and distinct, but there are at least several.

Provisionally, the position of this genus is determined by the superficial resemblance, in form of frond and pinnae, to the simply pinnate section of *Polystichum.* I do not believe that the affinity thus suggested really exists, but do not know where else to locate the genus. There is a distinctly stronger resemblance to some species of *Campium;* but the merging of stipe and rhizome does not encourage a reference to the Polypodiid group of genera.

12431. **Cyclopeltis** J. Smith, Comp. to Bot. Mag., 72:36, 1846.

The type is *Cyclopeltis semicordatum* (Sw.) J. Sm., *Aspidium semicordatum* Swartz, of which the type should be in Stockholm; this species is found in the West Indies and South America. Very close to this is *C. presliana* of the Malay region, of which *Aspidium Kingii* Hance, from the Caroline Islands is very likely a small form. Fée's genus *Hemicardion* is identical with *Cyclopeltis;* its description was accompanied by the description of several additional species, commonly regarded as synonyms of the two already listed. There is no

single character by which the plants of the two hemispheres always differ; but there are several distinct species.

12432. **Didymochlaena** Desvaux, Berl. Mag., 5:303, 1811.

The type is *Didymochlaena sinuosa* Desv., from the East Indies, regarded as synonymous with *D. truncatula* (Sw.) J. Smith, which is almost pantropic and is remarkably uniform in different lands. Desvaux' type should be in the Botanic Garden at Angers.

This and the preceding genus, *Cyclopeltis,* seem to me to be more nearly related to each other than to any other. There has been a great diversity of guesses as to the proper position of each in the fern system. *Cyclopeltis* has conspicuous elements of similarity to *Dryopteris, Polystichum,* and *Nephrolepis,* while *Didymochlaena* is apparently more isolated. Their distribution is evidence of considerable age. Taken with this, their uniformity is quite remarkable. The best I can now do with them is to regard them as together constituting a group coordinate with *Dryopteris, Polystichum,* and *Tectaria,* each of the last with its derived genera.

1244. **Tectaria** Cavanilles, Annales de Hist. Nat. 1:115, 1799.

This genus was set up to include the ferns previously referred to *Polypodium,* because they had round sori but were provided with circular indusia. It was exemplified by *Polypodium trifoliatum* L., which is accordingly the type species. *Aspidium* is a synonym, published a year or so later. The genus is clearly Dryopterid in origin, evolved by loss of dissection of the frond and consequent reticulation of the veins, the pattern being typically irregular, with free included veinlets (Sagenioid venation). In some species it is more regular, but not made up by the regular meeting of pairs of veinlets from adjoining veins (Nephrodioid venation). The parentage is not in *Nephrodium,* but in a free-veined section of *Dryopteris. D. dissecta* represents very well the point in *Dryopteris* from which *Tectaria* evolved. The genus has short, stout, more or less erect caudices, and large fronds, typically broad at the base. Indusia, typically present, are round-reniform. In the group which includes the type species, the basal lobes of such an indusium have grown together, so that the indusium is peltate; but the genus is not naturally divisible according to the shape of the indusium, and in species of various minor groups the indusium has been lost.

There are nearly two hundred recognized species, occurring throughout the tropics. It is evidently a genus of some age. The

distribution gives no good clue to its place of origin, but comparison of species with those of *Dryopteris* makes it possible to recognize, with much probability, those species as primitive which most resemble *D. dissecta,* and to suspect it of Oriental origin.

It is a genus notably rich in modern derived groups aberrant enough to merit generic recognition. Besides the several derived genera which follow, and a smaller number of them in the American tropics, it is almost certain that there are species evolved by a reversal of the evolutionary course which led to the genus—that is, species of Tectarid origin but with free veins. Such species are inseparable by definition from *Dryopteris,* and therefore are ascribed to that genus, though this is improper on sound principles of taxonomy.

12441. **Tectaridium** Copel., Phil. Jour. Sci., 30:329, 1926.

The type species is *Tectaridium MacLeanii* Copel., of which the type should be in the herbarium of the Bureau of Science in Manila. Two species are known, both from the eastern side of the Philippines. The genus is derived from *Tectaria,* from *T. decurrens* or some near ancestor of that species. It is characterized by pronounced dimorphism, with more or less complete loss of the lamina of the fertile fronds and the retention of the indusium—a very unusual combination of the two characters.

12442. **Hemigramma** Christ, Phil. Jour. Sci., 2C:170, 1907.

The type species, the only one cited in Christ's description, is *Hemionitis Zollingeri* Kurz, which is now regarded as a synonym of *Gymnopteris latifolia* Meyen. Goldman, the name becoming *Hemigramma latifolia.* It is a very common species in the Philippines, ranging at least to Java, and is one of the most variable of all ferns. In a recent monograph (Phil. Jour. Sci., 37:402, 1928) I have tentatively recognized seven species of *Hemigramma,* ranging from China and Formosa to Papua. *H. latifolia* may be regarded as the central species of the genus, being the most widespread, occupying the central area, and being subject to variation (or perhaps hybridization) in a manner which shows very close connection with a parent in *Tectaria,—T. crenata,* or a small group including *T. decurrens* and *T. crenata.*

Hemigramma has dimorphic fronds, and the sorus has extended, at first all along the veins, losing its indusium, and finally from the veins to the limited area between them. The single species, *H. latifolia,* is construed as including specimens with gymnogrammitoid and acrostichoid fructification, the latter being very common in fully

fruiting specimens. Whether the plant described and figured (in Phil. Jour. Sci. 3*c*:31, pl. 2, 1908) with distinct, indusiate sori, is an atavistic variant or an hybrid may not be decided and need not be. Construed in either way, it indicates the parentage of *Hemigramma.*

12444. **Quercifilix** Copel., Phil. Jour. Sci. 37:408, 1928.

The type and only known species is *Quercifilix zeylanica,* originally *Ophioglossum zeylanicum* Houtt. The generic discrimination was based on the study of specimens from Hong Kong. The species is reported from Mauritius to Borneo and Formosa; judging by the collections seen, it is commonest in southwestern China. It has a creeping, or finally ascending or suberect rhizome, clothed with broad, dark paleae. The fully developed but always very small frond is composed of a main terminal segment, subtended by a few basal pinnae which in less developed fronds are reduced to basal lobes. The venation is reticulate, with free included veinlets, as typically sagenioid as the small size of frond and segments permits. The fructification is at first gymnogrammitoid, and finally imperfectly acrostichoid, just as in *Hemigramma.*

The ancestry of *Quercifilix* can be located not merely in *Tectaria* but more definitely in the near affinity of *T. Labrusca,* an exindusiate species with rather small simple fronds and with pubescence on the fronds identical with that of *Quercifilix.* An extension of the sori along the veins is very common in exindusiate *Tectariae. T. Labrusca* cannot be regarded as itself the parent of *Quercifilix* because in its simple fronds and very narrow paleae it deviates farther than does *Quercifilix* from the general character of these structures in *Tectaria.*

12445. **Cionidium** Moore, Comp. to Gard. Mag. (1852), 143.

The type species is *Deparia Moorei* Hooker, Hooker's Jour. Bot., 4:55, pl. 3, 1852. The type specimen is in the Kew Herbarium. No other species is known. The position of the sori, carried on stalks beyond the margin, was responsible for the reference to *Deparia;* but the type of that genus is Athyriid, and so unstably modified that the genus can hardly be maintained. *Cionidium* is a *Tectaria* in all its vegetative characters. The cup-shaped involucre described by Hooker is a "decomposition product." Well preserved sori show a real indusium, and a rather scarious expansion of the lamina, the two grown together at the base, and only this basal portion remaining in age to give the appearance figured by Hooker. This indusium is

critically important; it proves that the ancestor of the plant, in *Tectaria,* was indusiate.

There is another Tectarid species, *T. Godeffroyi,* in Fiji, with the sori sometimes extra-marginal, though usually merely marginal. It is absolutely exindusiate. Its ancestors might have been indusiate or exindusiate; for an indusium has been lost in very many clearly known lines of evolution—as in this one too, but farther back. In this instance, we know that the immediate ancestor was exindusiate, because we know the ancestor—*T. latifolia.*[6] In New Caledonia, there is a *Tectaria* species, *T. Seemannii,* with sterile fronds indistinguishable from those of *Cionidium,* but with indusiate dorsal sori. The vegetative identity is so complete that it would be a mere affectation of caution to state it as other than a fact that *T. Seemannii* is the parent of *Cionidium.*

If the extra-marginal position of the sori of *T. Godeffroyi* were a fixed character, that too might well be treated as a distinct genus. It could not be combined with *Cionidium;* not because the indusium is a sufficient generic character, but because known different origin in the parent group would demand separate treatment. If there were many such phyletic lines, in which from various species or groups of species of *Tectaria* there had been an evolution of extra-marginal sori, the better policy would be to avoid the multiplicity of monotypic genera by extending the definition of *Tectaria* to include them all. At present, we know only *Cionidium* in which this peculiarity seems to be fixed, and *T. Godeffroyi* in which it is apparently in process of evolution.

12446. **Luerssenia** Kuhn, Bot. Centralb., 11:77, 1882.

The type species is *Luerssenia kehdingiana,* described from Lankat, West Sumatra, and from one specimen. I have never seen it. The sterile frond is said to be very like that of *Tectaria singaporeana;* the fertile is longer-stalked and more slender. The veins form rather regular areolae, each with one excurrent free veinlet bearing an elongate sorus and indusium.

125. **Athyrium** Roth. (Röm. Mag., 2^1:105, 1799) Tent. Fl. Germ., 3:58, 1800.

Although the title page is dated 1800, the actual publication of this part of the text of the Flora Germanica was earlier, and this was

[6] If this specific name is incorrectly applied, it does not affect the argument. There is a common Fiji fern called *T. latifolia,* with the dorsal sori typical of *Tectaria,* to which *T. Godeffroyi* is very similar except in the position of the sori.

probably the first publication of the name *Athyrium.* The two species first listed are both real *Asplenium,* from which genus and from *Polypodium* Roth was explicitly segregating a distinct group. The reasonable course is therefore to recognize as the type the sixth species, *A. Filix-femina,* of which the third, fourth, and fifth are synonyms. It is a very common fern of the northern hemisphere, accredited also to South America and Java. As I construe it, the genus owes its definition to Milde, who showed its distinctness from *Asplenium* in paleae, stellar structure of petiole, and otherwise; the identity of *Diplazium* and *Athyrium* in these respects; and the very intimate affinity of *Athyrium* and *Dryopteris.* The last is so close that no element of a definition will always separate the two genera. Typically, the sorus of *Athyrium* is elongate along the vein, while that of *Dryopteris* is not. But there are a number of species which are best assigned to one or the other on the basis of their affinity to other species more susceptible of generic identification, whereby we get *Athyria* with round sori and *Dryopteris* species with elongate ones. This occurs both among the species which may be near the common source of the two genera, and also among those far evolved from such a source. We recognize many small fern genera, the origin of which is absolutely known (*Haplodictyum, Mesochlaena, Cionidium,* etc., among those already treated; *Prosaptia,* discussed in the introduction), which we cut off from their parent genera by arbitrarily placed lines—lines which we shift, if we please, but still keep clearly drawn. *Athyrium* and *Dryopteris* are the only genera between which even an artificially clear-cut line cannot be drawn. They merge. But in their evolution they become so distinct and both so rich in groups of many species, that nobody would consider combining them because they merge.

The supposed distinction between *Diplazium* and *Athyrium* is that the former has more or less symmetrical double sori, occupying both sides of some of the fertile veinlets; the latter, sori bent across the veinlet, continuous from one side to the other at the upper end, and the two sides usually unequal. Most *Diplazia,* then, are coarse ferns and most *Athyria* are comparatively delicate. But in one after another of the natural groups of species there occur sori of both types, so that natural genera, defined by these characteristics, do not exist.

Athyrium is a genus of fully five hundred known species, distributed over the earth in very much the same proportion as ferns in

general. It includes many recognizable phyletic lines which have led to aberrant species, separable as small genera if one so choose, and mostly long since repeatedly so named. Among such groups or species with anastomosing veins are *Digrammaria* (*A. esculentum*), *Anisogonium* (*A. fraxinifolium* and others), *Diplaziopsis* (*A. javanicum*), *Callipteris* (*C. prolifera* = *A. accedens*) in the Orient, and *Hemidictyum* (*A. marginatum*) in America. The indusium has been lost in a considerable number of species. *Deparia* was based on an Hawaiian plant with sori borne beyond the margin of the frond, as in *Cionidium;* but the peculiarity seems to be too ill-established to serve for a specific distinction.

12521. **Blechnum** Linnaeus, Spec. Pl. (1753), 1077.

As to the type species, Linnaeus listed only two, *Blechnum orientale* from South America and *B. occidentale* from China. By common consent, treating the contradiction of names and regions as an accident, these names have been reversed. The two species are clearly congeneric, so that there is no doubt as to the nature of the genus. It contains about 175 recognized species, found in most parts of the world, but notably abundant in far southern lands, as though once best developed on the Antarctic continent. Its proper location in the fern system is not yet acceptably settled. It has some striking features in common with the larger and coarser species of *Athyrium* which suffice to make probable some affinity of the two. The occurrence of atavistic variants indicates that the anastomosing fertile vein of *Blechnum* originated, in phylogeny, from the succession of lowest acropetal veinlets, which are the ones most constantly fertile in *Athyrium.* On the other hand, *Blechnum* would seem on some grounds—distribution, and structure of sporangia—to be an old and even, as *Polypodiaceae* go, a somewhat primitive genus, not hastily to be associated with any specialized group in *Athyrium.*

Bowers' opinion, that it has come down from a Cyatheoid ancestor, independent of *Dryopteris* and *Athyrium,* is possibly correct. His further belief that this descent was routed by way of something like *Matteuccia* is less acceptable, coupled as it has to be with the hypothesis that *Lomaria* is more primitive than *Eublechnum,* and the fantastic corollary that the lamina of the fertile frond of *Eublechnum* is an organ *sui generis,* not homologous with the leaf expansion of other ferns, nor apparently with that of the sterile frond of the same individuals.

12522. **Doodia** Brown, Prod. Florae Nov. Holl. (1810), 151.

The type species is *Doodia aspera.* There are perhaps six properly recognizable species, with the center of distribution in the Australian-Polynesian area, only one in Malaya and Ceylon. *Doodia* is most like one section of *Woodwardia* in the used diagnostic characters, but is closely related to *Blechnum,* with which it shares the peculiarity of apparent southern origin.

12523. **Brainea** J. Smith, Cat. Kew Ferns (1856), 5.

The single species, *Brainea insignis,* is now known from Khasya, China, Sumatra, and Mindoro, everywhere apparently on land subject to fires. It is Blechnoid in aspect, with a very stout, erect trunk, but with naked and indefinite sori. The anastomosis of the veins to form costal areolae is irregular, in a manner making it manifest that each areola is bounded on the outside by the lowest acropetal veinlet. In this respect, it is more primitive than *Blechnum,* while it is farther from any probable parent genus in its Grammitidoid fructification. With the same lack of certainty, I treat it like *Blechnum,* as Athyriid.

12524. **Woodwardia,** J. E. Smith, Mém. Acad. Turin, 5:411, 1793.

The type species was *Acrostichum areolatum* L., of the eastern United States. There are probably nine known recognizable species disconnectedly scattered over the northern hemisphere and south to Java, five of them in the Orient. The genus is construed here as parallel to *Blechnum* in origin.

12525. **Sadleria** Kaulfuss, Enum. Fil. (1824), 161.

The type is *Sadleria sadlerioides* Kaulf. The genus is composed of perhaps five variable species, confined to the Hawaiian Islands. Christensen regards one of these as a depauperate *Polystichum.* The others, including the type, are tree ferns, probably related to *Blechnum,* but possibly to *Woodwardia.*

1253. **Asplenium** Linnaeus.

A genus of more than six hundred species, world-wide in distribution.

The status of this genus is puzzling in every respect. As a matter of formal taxonomy, its type should be fixed by arbitrary authority, for there is no clear rule which will select one included in the genus as now recognized. As to its place in classification, it was easily located as long as the fructification, or this and the venation, provided

the only characters held in any respect, and "affinity" was a figure of speech. The precedent of almost all fern literature associates it with *Athyrium,* and the two are thoroughly confused by Bower even in 1928.

Actually, it is an exceptionally natural genus, although in some respects the most diversified in the family. While other genera are typically terrestrial or epiphytic, and most of them are exclusively one or the other, *Asplenium* competes for a place in both habitats, without evident choice. It includes a considerable number of evident phyletic groups and series, and several of these are common to the eastern and western hemispheres. The great diversity of adaptation and the wide distribution of the subordinate groups mark *Asplenium* as an old genus. I have not been able to fix on any one of its elements as clearly primitive, and until this is done can only assign it a place on the old basis of general resemblance. This ties it to *Athyrium.*

Many genera have been proposed as segregates of *Asplenium,* but its natural minor groups are too ill-defined for convenient recognition. Even such highly specialized groups as *Darea* and *Thamnopteris* are reached through continuous series, and neither is easily definable as a natural group. Under such conditions, I prefer to leave them in *Asplenium.*

125311. **Ceterac** Adanson, 1763, or **Ceterach** Willd., 1809–10.

Whoever is accepted as authority for this genus and the spelling of its name, the type is *Asplenium Ceterach* L.; Adanson, however, took it from Tournefort and his (Adanson's) type is in the Paris Museum.

A genus of four species, of which two are found in the Himalayas. It is ill-distinguished from *Asplenium.* In the type species the indusium has disappeared, replaced in its protective function by a dense layer of paleae; but one of the species included in *Ceterach* because of obvious affinity has the indusium well developed.

125312. **Pleurosorus** Fée, Genera Filicum (1840–52), 179, pl. 16*c*.

The type should be Fée's specimen of *Pleurosorus ciliatus,* now regarded as *P. papaverifolius,* a native of Chile. A second species, *P. rutifolius* (R. Br.) Fée, occurs in Australia and New Zealand, and Diels has referred to this genus one species from Spain. As Fée stated, *Pleurosorus* is an exindusiate *Asplenium,* clothed with hairs; at any rate, our present knowledge does not justify placing it elsewhere.

12532. **Camptosorus** Link., Hort. Berolin. Deser. (1833), 69.

The type is *Asplenium rhizophyllum* L., which the application of one rule would make the type of *Asplenium.* Besides this species of the eastern United States, there is one other, *Camptosorus sibiricus,* in Siberia, China, and Japan. The origin is patently boreal. The Asplenid nature of *Camptosorus* is clear, even to the location of approximate specific origin of the type species, in the parent genus.

C. rhizophyllus is like *A. pinnatifidum* in such specific characters as those of the paleae, color of the base of stipe, and the attenuate, sometimes rooting tip. This source is not obscured by drawing the line between the genera on the other side of *A. pinnatifidum* (as Diels did), for that species has its manifest relatives in *Asplenium;* and such a transfer leaves the daughter genus in this case quite undefinable from the parent.

125331. **Phyllitis** Ludwig, 1757.

Ludwig is said to have based his genus on a description by Tournefort; the plant is *Asplenium Scolopendrium* L., a fern found in most of the cool parts of the northern hemisphere and surely of boreal origin. The genus has been made to include isolated species in various other regions. Its diagnostic soral character is, as in the case also of *Camptosorus,* such as might very easily be consequent on simplification of the frond; it is, therefore, more reasonable to suppose that this character has evolved independently more than once, and from local sources in *Asplenium,* than to try to account otherwise for the discontinuous distribution of *Phyllitis.*

125332. **Diplora** Baker, Jour. Bot., 11:235, 1873.

The genus was based on a specimen named *Diplora integrifolia,* from the Solomon Islands, which I have construed as synonymous with *Phyllitis Durvillei* (Bory) O. K. I demonstrated the approximate specific source of this fern and its Malayan relatives years ago (Phil. Jour. Sci., 8C:147, 1913). As shown particularly by their ontogeny, but also by every other available test, they are derived from such a fern as *Asplenium epiphyticum.* Baker's generic distinction from *Phyllitis* was an illusion; wherefore, treating a genus as a group with definable characters, I reduced these ferns to that genus. I do not suppose, however, that *Phyllitis Scolopendrium* originated at this point in *Asplenium;* and am therefore unable, treating origin as the most essential element of generic character, to continue to regard these ferns of the Oriental tropics as congeneric with it. The next distinctive name available for them is *Diplora.*

The base of the frond provides a formal generic distinction between *Phyllitis* and *Diplora.* This will appear very trivial to those accustomed to dependence upon a certain set of formal criteria for the distinctions between genera. If, however, we remember that the essential basis of distinction is always in phylogeny, and that the formal criteria are at best, in their real nature, only marks serving for facile recognition, the form of leaf-base may be welcomed as an exceptionally convenient mark of this kind. In this case, we deal with parallel evolution. Evolution may be convergent, and leave us with no convenient mark whatever—see the remarks under the following "genus."

125333. **Boniniella** Hayata, Bot. Mag. Tokyo, 41:709, 1927.

The type is *Boniniella Ikenoi,* from the Bonin Islands; I have not seen it. It was first described as *Scolopendrium,* and Hayata treats it as related to *Camptosorus.*

This is a third genus parallel in evolution to the two preceding. The alternative to the recognition of these genera is their inclusion in their common parent, *Asplenium.* As *Asplenium* is a very large and diversified genus without them, it would probably be better to retain all three than to expand *Asplenium* so as to include them. Unfortunately, as regards our convenience, the field is not yet exhausted. *Phyllitis Delavayi* and *Asplenium cardiophyllum,* both Chinese, appear to stand in the same relation as *Phyllitis Scolopendrium* and *Asplenium pinnatifidum. P. Delavayi* is not apparently congeneric with *P. Scolopendrium,* but is equally worthy of generic rank. It can give us a fourth genus, all four definable alike by the use of the usual terms of generic definitions. If we follow this course consistently, we will have a fifth such genus in Mexico and a sixth in Brazil; no others are known to me *now.* Confronted by this situation, my preference is very decidedly to construe *Asplenium* as including them all. I have listed *Phyllitis, Camptosorus, Diplora,* and *Boniniella,* only because their presentation emphasizes the situation and requires no new names.

12534. **Diellia** Brackenridge, U. S. Expl. Exped., 16:217, 1854.

The type species is *Diellia erecta.* The entire genus of perhaps nine species is endemic in Hawaii. Because of the superficial similarity of several species to *Lindsaya,* they have always been reduced to that genus or treated as its relatives. Only *D. Mannii* has been recognized, by Kuhn and by Christensen, as related to (*Loxoscaphe*) *Asplenium.* The genus seems to me to be a natural one and to include that species, and to be related in its entirety to *Asplenium.* The stem is short,

more or less erect, and clothed with scales like those of *Asplenium*, but unlike those of such Dicksoniid ferns as bear any scales at all. Some of the species have the rachis scaly, a phenomenon common in *Asplenium* but unknown in any relative of *Lindsaya*. Because the species with simply pinnate fronds have anastomosing veins and approximately marginal sori, while the *Asplenium* species with fronds of similar form are essentially different in these respects, I vision the genus as evolved from an ancestor in *Asplenium* with much dissected leaves, and the sorus apparently marginal because the size of the segments leaves no other possible position. The evolution of the species of *Diellia* has been by a progressive simplification of the frond, in which the sorus remained near the margin, and the veins, merely as in many other phyletic lines, united as the intact area of lamina became ample enough to let them unite.

12535. **Stenochlaena** J. Smith, Hooker's Jour. Bot., 3:401, 1841, name and citation; 4:141, 1841, description.

The type of the genus is the Philippine plant discussed by Smith in the first publication of the generic name, Cuming No. 133. This was said to be "*Acrostichum scandens* L.," but there never was a species so named. The name now used is *Stenochlaena palustris* (Burm.) Bedd. About forty species from all parts of the tropics are now referred to the genus, which is not so surely homophyletic as could be desired. The type, as described by Smith, is cognate in Aspleniid origin with *Diplora*, as is very plain when the polymorphism of the fronds of immature plants is compared with the polymorphism of the fronds of *Asplenium epiphyticum*. The affinity is so absolutely clear that Christ felt constrained to regard this *Asplenium* as a *Stenochlaena* with arrested development. Just as results from the transfer of *Asplenium pinnatifidum* to a daughter genus, the effect is to make the latter altogether indefinable. Other Philippine species are more conspicuous than *S. palustris*, by the production of a series of compound juvenile forms.

In seeking to derive *Stenochlaena* from *Blechnum*, Bower (Ferns, 3:177) ignored this evidence from ontogeny, although acquainted with Christ's publication on the subject. And his general statement, that "The cumulative effect of all the evidence, foliar morphology, anatomy, soral and sporangiate structure, is to show that *Stenochlaena* is a Blechnoid type which has assumed a climbing habit and an Acrostichoid, non-soral state," rested on a very imperfect acquaint-

ance with the ferns. Unless it be the sporangial structure, which is itself by no means Blechnoid, there is no one of these respects in which *Stenochlaena* is essentially unlike indisputable species of *Asplenium.*

12536. **Lomagramma** J. Smith, Hooker's Jour. Bot., 3:402, 1841; 4:152, 1841.

The genus was based on *Lomagramma pteroides,* collected in Luzon by Cuming, since regarded as a synonym of *Leptochilus lomarioides* Bl. There are at least ten known species, not all named in this genus, ranging from southern Polynesia across Malaya and probably to the Mascarenes. They are large, freely scandent ferns, the stout, scaly rhizomes containing a loosely reticulate vascular system; fronds pinnate or more compound with the leaflets articulate to the axes, dimorphous, with more or less completely acrostichoid fructification; except in species with leaflets too small or too cut to provide the opportunity, the venation is reticulate, in the manner of *Syngramma* and *Acrostichum,* without included veinlets. *L. lomarioides* bears peculiar paraphyses, which are wanting in *L. articulata.*

The genus has been a very difficult one to place in the systematic arrangement of genera. At different times, I have tried to locate it in the Dicksoniid series, and among the derivatives of *Phymatodes.* The paleae exclude it from the former, even more surely than the dictyostele. My present disposition is to regard it as Aspleniid. The spores (of *L. articulata*) and the pedicels of the sporangia suggest this affinity, as do also the paleae. This assignment to a place makes the genus approximately cognate with *Stenochlaena,* where, however, its position is only a tentative one.

12537. **Thysanosoria** Gepp, *in* Gibbs, Dutch New Guinea (1917), 193.

The type is *Thysanosoria dimorphophylla,* from New Guinea. I have not seen it and can only guess at its proper location. Gepp says, "The systematic position, in view of the exindusiate sori and the non-articulate stipes, would seem to be near to *Phegopteris,* though the plant recalls *Stenochlaena* in its climbing habit and dimorphous fronds, and *Nephrolepis* in its articulated pinnae." Several of the items in the description are suggestive of *Lomagramma.*

20. **Dicksonia** L'Héritier, 1788.

As the genus is usually construed, its type is *Dicksonia arborescens,* and I am treating it as thus fixed. Observance of the rules usually followed in these questions will reverse the names of the genera here

called *Dicksonia* and *Balantium,* as the latter is broadly construed, and by any construction will make *Balantium* the name of the genus here discussed.

We begin here the enumeration of a second great series of genera which, from a common origin not yet agreed upon, has evolved independently of the *Cyathea–Dryopteris* series. If Polypodiaceae be broken up into smaller families, no member of one of these series, unless it be the most primitive, can properly fall in the same family as any member of the other series. The Dicksoniid ferns, as a group, are characterized by marginal sori, creeping rhizomes, closed vascular bundles, and hairiness instead of scaliness. Many of the genera are aberrant in one or more of these respects.

As in the Cyatheid series, there has been an evolution from the more primitive representatives, with large, stout-stalked sporangia, maturing together, and with the annulus oblique, to more numerous and recent genera with smaller, longer- and more slender-stalked sporangia, ripening in succession and with longitudinal, interrupted annulus. Whether this parallel evolution (which has been gone through in yet a third series, the Dipterid ferns) has been really independent to the extent that the variation which might provide the material for selection has occurred afresh in each respect in each phyletic series, or whether hybridization across the line between the series has enabled one of them to use a variant character appearing in the other, may not be guessed even on the basis of known evidence. With the qualification that the parallelism might have this explanation, as might also a few instances of genera not clearly fitting into the series as we now know them, we are justified by our present knowledge in treating them as true phyletic lines, separable by a line far more true to nature than that which has been in use, cutting across both of these series, to separate Cyatheaceae and Polypodiaceae.

In the group which is given its name, *Dicksonia* retains primitive character in its reproductive structure, but is aberrant and specialized in its stout, erect trunk and correlated stellar structure. With these, it cannot be regarded as representing the ancestor of the series as a whole.

It is a genus of some twenty-four currently recognized species, not all very distinct, mostly native of the southern hemisphere. Probably because of the remarkable development of a thick layer of roots running down outside of and encasing the stem, they endure a colder climate than any other tree ferns.

21. **Cibotium** Kaulfuss (Jahrb. d. Pharm., 1820), Enum. Fil. (1824), 229.

The type is the Hawaiian *Cibotium Chamissoi.* There are a few other species in Hawaii and in Mexico and Central America. In the Orient—China to Sumatra and the Philippines—is one species, *C. Baranetz,* variable enough to have several names, or a small group of hardly distinguishable species. Less distinctively arborescent than *Dicksonia,* from which it is distinguishable by the greater specialization of the leaf segment which bears and protects the sorus, and by several peculiarities in aspect which singly would seem insignificant; but nearer to *Dicksonia* than to any other genus and, like it, an offshoot from the series as a whole.

22. **Cystodium** J. Smith, (Hooker's) Genera Filicum (1841), pl. 96; London Jour. Bot. 1:433, 1842.

The type is *Dicksonia sorbifolia* J. E. Smith, described from the Moluccas. *Dicksonia papuana* is congeneric with it, and perhaps identical. Both are nearly related to *Dicksonia,* distinguished by the less oblique annulus (it is imperfectly longitudinal) and smaller, simpler leaves. The hairiness is essentially identical. The caudex seems never to have been described and my specimens do not show it; judging by the fronds, I would suppose it to be stout and probably erect. No other oriental genus is so near as this to *Dicksonia. Thyrsopteris,* known only from Juan Fernandez, is a monotypic genus, unmistakably related to *Dicksonia,* as shown by the type of leaf and the hairs, but more like *Cyathea* in sporangia and protection of sorus. Of surviving ferns, it best represents the common parentage of the Dicksoniid and Cyatheid series of genera.

2211. **Nephrolepis** Schott. "Genera Filicum t. 3 (1834)."

The type is said to be *Aspidium biserratum* Sw., a common fern of wide range in warm countries. Like several others of its genus, it is not well fixed in its specific characters. Perhaps twenty species are recognized; the number is a matter of choice. *Nephrolepis* is one of the most natural of genera in its vegetative aspect and characters, and the most varied of fern genera in those of its sorus, which is marginal or dorsal, single and isolated or confluent with its neighbors, with indusia suggesting those of *Dryopteris, Tectaria, Humata, Schizoloma,* and *Dicksonia.* Internally, however, the structures of the sorus are uniform enough. The spores are oblong to reniform-oblong, and

rough; sporangia flattish, long-stalked, with annulus of about fourteen cells, and ill-differentiated stomium. Suggestive features are redness of all walls in the soral structures and some warping of the sporangia. In two species, I have found aberrant sporangia with the annulus really oblique.

Nephrolepis has been placed here and there in the fern system. In spite of bearing scales, and of the Aspidioid indusia of the commoner species, it quite surely belongs in the Dicksoniid group. I agree with Christensen (in litt.) that the Bornean fern I tentatively placed here as *N. marginalis* should be excluded. The resemblance, however, is real, and I still believe that the most probable more primitive relative of *Nephrolepis* is *Cystodium.* This is not the first known fern with enough resemblance to both to attract attention; the species now called *N. abrupta* was first described as a *Dicksonia* and its resemblance to the type species of *Cystodium* has been noted repeatedly. The affinity of *"N." marginalis* to *Cystodium* is unmistakable. While I do not care to widen the concept of *Cystodium* enough to admit it, I am giving it no other name because of a suspicion that the proper genus has already been named—(221) *Leptopleuria.*

230. **Orthiopteris** Copeland, Bishop Museum Bull., 59 : 14, 1929.

The type is *Orthiopteris ferulacea, Davallia ferulacea* Moore. The generic diagnosis was based on a specimen collected by Gillespie, No. 3326. The species is known only from Fiji. It has an erect caudex clothed with dark bristles but without scales. The fronds are deltoid, quinquepinnatifid, with narrow, one-nerved ultimate segments. Sori terminal on the veins, submarginal, and indusium conical, with the sides affixed. Spores globose-tetrahedral and conspicuously sculptured. The hairiness and form of indusium and its position on the vein place this fern clearly in the Dicksoniid series; the erect caudex suggests affinity to *Dicksonia.* The caudex, the spores, and the indusium are particularly like those of the following genus, which, in being scaly, is still more aberrant from the general character of the series.

231. **Ithycaulon** gen. nov.

Caule erecto, paleis tecto, systemate vasculare reticulato; radicibus validis nudis; frondibus decompositis, pinnulis obliquis; soris submarginalibus ad apices venularum, paraphysibus carentibus, indusio conico ad latera adnato, receptaculo in sorum protenso, sporangiis majusculis annulis longitudinalibus subsymmetricis, sporis orbiculari-tetrahedricis, sculpturatis. Genus Saccolomate affine sed eodem char-

acteribus notatis segregandum. Typus, **I. moluccanum,** *Davallia moluccana* Blume, Pterid. Philippin. Exsic. No. 67 in Herb. Copeland demonstratum. Species aliae; **I. caudatum** (*Saccoloma caudatum* Copel. Phil. Jour. Sci., 30:327, 1926; **I. inaequale** (*Davallia inaequalis* Kze. quoad specimina visa et descr. Maxonii, Pterid. Porto Rico (1926), 491; sed planta Kunzii caudicem repentem habuerit).

The genus *Saccoloma* of Diels and Christensen is made of not less than four too distinct elements: (1) *Saccoloma,* typified by *S. elegans,* an American fern with large, simply pinnate fronds, broad sori and densely hairy roots; (2) *Cystodium,* very near to *Dicksonia,* confined to the Old World; (3) the group here removed, *Parasaccoloma* Keys., pantropic; and (4) *S. imrayana,* likewise simply pinnate but distinct from *S. elegans* in characters of sporangium and spores, as well as in form and protection of sorus, and slender rhizome. I have not adopted *Parasaccoloma* as a name, chiefly because I would not know with sufficient confidence what typified it. The affinity of *Ithycaulon* and *Saccoloma* is almost proved by the similarity of their sporangia and spores. Both have fairly large, somewhat angular, decidedly reddish sporangia, with well defined but not exceedingly dilated stomium supported by thin-walled cells, the thickened cells numbering fifteen to nineteen in *Ithycaulon* and fourteen or fifteen in *Saccoloma.* Both have regularly sculptured, globose-tetrahedral spores.

In spite of its trunk and dictyostele, and the harsh paleae on the apex of the stem, I include *Ithycaulon* in the Dicksoniid series. The fronds and the sori are too distinctively like those of *Dennstaedtia* and *Microlepia* to be other than valid evidence of affinity; and the resemblances to *Saccoloma,* already noted, show its connection with this general group in some of the features in which it is unlike *Dennstaedtia.*

24. **Balantium** Kaulfuss, Enum. Fil. (1824), 228.

As already noted, under *Dicksonia,* the proper type of this genus would be a plant now treated as a *Dicksonia.* The other species listed by Kaulfuss, *Balantium Culcita,* must be the type if the first one is not; it is the species which would properly typify *Dicksonia.* The three feebly distinguished species occupying the area from New Zealand to Luzon would better be removed from *Balantium,* but have no other appropriate generic name. They are "Chaetopterides" (a name given by Kuhn to the ferns bearing hairs, in distinction to scales), with stout but not erect stems, hairy leaves, sporangia with imperfectly longitudinal but usually interrupted annuli, and oblique

ultimate pinnules. They are related to *Dennstaedtia,* but more primitive in their sporangial characters.

241. **Dennstaedtia** Bernhardi, Schrader's Jour. (1800[2], vero 1801), 124.

The type species is *Dennstaedtia flaccida, Trichomanes flaccidum* Forst., of Polynesia. There are about seventy-five recognized species, tropical and extra-tropical, in both hemispheres. The genus was long merged in *Dicksonia,* with which it agrees in its marginal sori and some modification of the margin for the protection of the sorus; but its creeping rhizome and interrupted annulus, coupled with the different frond-form and texture and smaller sporangia, produced in sequence, show that the affinity, while real, is not very close. It is nearer to *Balantium,* which also was formerly included in *Dicksonia.* Of the several phyletic groups recognizable within *Dennstaedtia,* one leads unmistakably to *Hypolepis;* and there may be more than one line leading into *Microlepia.* Its affinity to *Dicksonia* and *Balantium,* which are clearly more primitive; its own somewhat primitive features—such as "gradate" sorus—and its perfect combination of the characters recurring throughout the series in less complete combination or less typical development; and its world-wide distribution, all mark it as fitly representing the common ancestor of the largest similarly homogeneous group of Polypodiaceous genera.

2411. **Microlepia** Presl, Tent. Pterid. (1836), 124.

The accepted type is *Microlepia Speluncae;* but the first listed and the first figured by Presl are both apparently members of the group I have removed from *Saccoloma* and named *Ithycaulon.* Strict observance of one rule would therefore make *Microlepia* the proper name of that genus. Construing it as typified by *M. Speluncae,* it is a genus of forty-five or fifty recognized species, ranging from a center in Malaya to Madagascar, Japan, Hawaii, and New Zealand, with *M. Speluncae* reaching around the world. It is typically distinguished by the withdrawal of the sorus from the margin, and an enlarged receptacle bearing the sporangia. It includes a few aberrant species with less cut fronds, or with glabrous and coriaceous fronds; but the body of the genus is much like *Dennstaedtia* in aspect, and in some species merges fairly into it. If this happens in only one phyletic line, it raises no objection to the continued recognition of both genera; but if it is found to occur in plural lines it would be better to give up *Microlepia* as a genus.

24111. **Oenotrichia** gen. nov.

Genus Microlepiae affinis specierum quondam sub Leptolepia errore collocatarum; rhizomate repente stipiteque rhachibusque pilis vinicoloribus obsitis; fronde pinnatim decomposita segmentis vel pinnulis ultimis latis, soris dorsalibus ad venulas apicalibus, indusio basifixo lateribus liberis. Typus specificus, **Oenotrichia maxima** (Fournier), *Leucostegia maxima* Fournier, Ann. Sc. Nat. Bot. *V.* 18 (1873), 344, specimen ex Herb. Mus. Par. s.n., "donné par M. Pancher, 1870," in Herb. Univ. Calif., No. 361314.

This genus retains in their entirety the vegetative peculiarities common to *Dennstaedtia* and *Microlepia,* but with an indusium so different that the real affinity has been overlooked. This indusium is, as stated in the diagnosis, fixed at the base and free on the sides. In greater detail, the indusia are not uniform on the type specimen. Some are cordate, fixed by a medial basal point, as described by Fournier; others are broadly reniform and others semiorbicular; and the attachment may be by a "point," i.e., to the vein only, or it may extend laterally beyond the vein. There is no near affinity to *Leucostegia;* and that to *Leptolepia* is indirect, extending back through *Microlepia* to *Dennstaedtia* and thence to *Leptolepia.*

Other species referred to *Leptolepia* on the basis of similarity of indusia, but in violation of phylogeny, are:

O. tripinnata (F. v. M.) = *Davallia tripinnata* F. Muell. Herb. *in* Bentham Fl. Austral., 7:717, 1878. The proper location shown by "obovate obtuse lobes" and "sori . . . . under the sinus."

O. Novae Guineae (Ros.) = *Davallia Novae Guineae* Ros., Fedde's Rept., 5:36, 1908, specifically distinguished by the naked lamina.

Kuhn's figures of "*L.*" *aspidioides,* illustrating *Leptolepia,* apply not to that genus as typified by *L. Novae-zelandiae,* but to an *Oenotrichia.* The specific name was never properly published.

24120. **Tapeinidium** (Presl) Christensen, Index Fil. (1906), 631. *Microlepia* § *Tapeinidium* Presl, Epim. Bot. (1849), 94, 96.

The type species is *Tapeinidium pinnatum* (Cav.) C. Chr., described from Luzon and found from Malaya across Polynesia, the entire range of the genus. The number of species is from six to many, depending upon how wide a range of forms is included in *T. pinnatum.* As a subgenus, Presl distinguished this from *Microlepia* proper by the location of the sorus on a very short veinlet, which brought it farther from the margin, and by three vascular strands instead of one horseshoe-shaped one in the stipe. With the inclusion of recently discovered

species in Papua and Sumatra, which are certainly members of the same natural group, the former character must be abandoned, but the group remains very distinct from *Microlepia.*

24121. **Sphenomeris** Maxon, Jour. Wash. Acad. Sci., 3:143, 1913.

The type and only known American species is *Sphenomeris clavata, Adiantum clavatum* L. There are two widespread species in the Old World and several others of more local occurrence. Typically, *Sphenomeris* has decompound fronds with cuneate ultimate pinnules or segments, bearing simple or fused apical sori. As a natural group, it is very close to *Tapeinidium,* and in New Caledonia there are several species which seem to belong to it, but are not sharply cut off from others apparently referable to *Lindsaya,* to which genus all of them were first ascribed.[7]

24122. **Protolindsaya** Copeland, Phil. Jour. Sci., 5C:283, 1910.

The type and only known species is *Protolindsaya Brooksii,* endemic in Borneo, its type in the author's herbarium at the University of California. This little fern presents a combination of features better known in *Ithycaulon, Sphenomeris, Tapeinidium,* and *Lindsaya.* How far this combination is evidence of affinity to all of these, as I construed it when publishing the genus, and how far it may be a mere consequence of reduction of stature, is an open question. My present judgment is that its nearest affinity is to *Tapeinidium,* from which it may have been derived by reduction and correlated modification. The paleae are distinctive, but still of the general type of those of *Tapeinidium, Sphenomeris,* and *Lindsaya,* derived from the hairs typical of the Dicksoniid series, and far less aberrant than are the harsh paleae of *Ithycaulon.*

24123. **Lindsaya** Dryander, *in* Smith, Mém. Ac. Turin, 5:413, 1793.

The type given by Christensen (Index, XXX) is *Lindsaya trapeziformis* but the only species cited by Smith is *Adiantum guianense* Aubl. The genus includes some one hundred and thirty recognized species, in the tropics of both hemispheres but best developed in the Orient. It is apparently a natural genus, the allocation of considerable parts of it to other genera (*Davallia, Saccoloma*) by various authors being in violation of nature, and not even reflecting affinity. It is like *Asplenium* in its adaptation to both terrestrial and epiphytic

[7] The argument presented in the case of *Goniophlebium,* page 109, does not apply to *Odontosoria,* in the publication of which Fée completely ignored Presl's prior use of the same word as the name of a subgenus. It is *Odontosoria* Fée, not *Odontosoria* (Presl) Fée.

life. The terrestrial species usually have the fronds rather crowded, but the rhizome is always creeping, and its bundle system is either a solenostele, except when too congested, or is solid, and then probably derived from a solenostele. The vestiture of the rhizome is almost always of paleae, but these are thin and usually narrow, of the type found in *Tapeinidium,* etc., evidently derived from the dark reddish hairs of the Chaetopterid ferns. In some species, as the New Caledonian *L. nervosa,* only these hairs are present, and in some others the paleae intergrade with hairs. *Lindsaya* is related to *Tapeinidium* and *Sphenomeris.* It seems also to be related to *Schizoloma;* but this appearance owes much of its force to the inclusion in the latter genus of an element which would better be returned to *Lindsaya.* The diversity and distribution of *Lindsaya* are in themselves evidences that it is an older genus than *Tapeinidium* and *Sphenomeris,* and its vascular structure has been construed as primitive. However, regarded as a properly Polypodiaceous fern, it is more specialized than *Tapeinidium* and less like any probably more primitive member of the Dicksoniid series, and attempts to relate any Polypodiaceous genus directly to either Gleicheniaceae or Schizaeaceae demand the supposition of convergent evolution in too many respects to enlist my sympathy.

Included in *Lindsaya* are *L. microphylla* and a few other species of the New Caledonia-Australian region, which seem fairly on the line between *Lindsaya* and *Sphenomeris.* Gaudichaud, in Freycinet, Voyage autour du Monde, Bot., p. 379, proposed a genus *Hymenotomia,* which would have been typified by the species just named, but did not formally publish it.

My judgment is that *Lindsaya* is a genus cognate with *Tapeinidium* and *Sphenomeris,* but far more successful, the surviving evidence being in two minor groups (those of *L. nervosa* and *L. microphylla*), both found in and near New Caledonia, which may therefore be its most probable original home.

24130. **Schizoloma** Gaudichaud, Ann. Sci. Nat., 3:507, 1824.

The type is *Schizoloma cordatum.* About twenty species are recognized, in the tropics of both hemispheres, falling into natural groups which are not very positively congeneric. One element included is certainly very near to *Lindsaya. S. heterophyllum,* originally described in that genus, is like it in many respects, notably the stelar structure of its rhizome. Similar are also the much-named *S. ensifolium, S. Vieillardii,* and others with thin leaves. The coriaceous

species, including the generic type, are a more clearly marked group. In both groups are species of peculiar frond-forms, duplicated in *Syngramma,* to which genus affinity is apparent, in spite of different stelar structure in the species which have been examined. No other indusiate genus serves as well as *Syngramma* to connect the exindusiate genera, which follow, with the more primitive Chaetopterids. This connection is shown by the elongate and coalescent sori, besides the similarities in form, and other features common to the series as a whole.

24131. **Taenitis** Willdenow, "Sprengel, Aubit., 3:372, 1804."

This genus was published, as on Willdenow's authority, by Sprengel, Swartz, and Schkuhr, before Willdenow himself. As it was long regarded as monotypic, there is no question as to the type, *Taenitis blechnoides,* which occurs throughout the eastern tropics. I have already explained its position in the fern system (Phil. Jour. Sci., 7C:47, 1912, and later efforts by Goebel and Bower are explicable by their not knowing its relatives. Its affinity to *Syngramma* and *Schizoloma* is so manifest that the propriety of recognizing so many genera is the only thing remaining in doubt. The type species is a variable fern, especially in the width of the pinnae and the location of the sori; it may well include *T. stenophylla* Christ, as Christ suggested.

Whether any species with simple fronds, of which several have been ascribed to it, are best construed as *Taenitis,* I leave as an open question, with which it is understood that Christensen is at present occupied.

Without hesitancy, I now include in *Taenitis* as **T. requiniana** (Gaud.) n. comb., the plant which has been regarded as constituting the genus *Platytaenia.* A discussion of this case will emphasize, and may serve to clarify the basic principles of classification and nomenclature. Kuhn closed his publication of this genus with the following sentence.

Es dürfte vielleicht für die Zukunft eine mit Nothwendigkeit sich ergebende Consequenz sein, Platytaenia und Taenitis zu einer Gattung zu vereinigen trotz ihrer sehr verschiedenartigen Fructification; denn wenn wir einmal den Schritt gethan haben Arten mit verschiedener Ausbildung der Fruchthaufen zu einer Gattung zu vereinigen, um habituell begrenzte Gattungen zu erhalten, (z. B. Ceterach officinarum und Asplenium alternans Wall., sowie beschleirte Aspidium- und unbeschleirte Phegopterisarten) so ist nach meiner Ansicht es eine nothwendige Consequenz, dass, falls nicht sonstige unterscheidende Merkmale noch vorhanden sind, auch Gattungen zulässig sind, in welchen die einzelnen Arten eine so verschiedenartige Ausbildung der Fructification aufweisen, wie bei Taenitis und Platytaenia.

I recognize no cogent rule ("mit Nothwendigkeit sich ergebende Consequenz") which would demand the generic union of groups differing in but one respect, or the separation of those differing in more than one. If there were such a rule, its application would leave us very free in the exercise of personal judgment; for correlated differences may be construed as one or as several. Some variation in the sorus, instead of being unusual, is found in many genera, in most of the large ones, *Cyathea, Dryopteris, Tectaria, Athyrium, Lindsaya, Adiantum, Nephrolepis, Campium, "Grammitis,"* for examples. The sorus never suffices for the characterization of a group unless the group is a phyletic entity.

Platytaenia is to be reduced to *Taenitis,* not because the Acrostichoid fructification *might* not be a sufficient distinction, but because no such distinction exists. *Taenitis blechnoides* varies notoriously in width of pinna and position of sorus. The latter may be so close to the costa that but little lamina separates them, or so close to the margin that a very narrow sterile strip is beyond it. It is not unusual for fertile pinnae to be narrower than sterile pinnae on the same plant. And the sorus is no mere line; it always has width, which very commonly exceeds that of the vein on which it originates. *T. requiniana* is distinguished by more pronounced dimorphism, the difference being in the reduction of sterile lamina, rather than in the sorus. The original drawing of the species depicts the sporangia as completely covering the nether surface; but a fragment of Lesson's collection (from Waighiou, cited by Kuhn) kindly sent me from the Berlin Herbarium, shows a sterile margin no narrower than that of one of the pinnules shown on plate 2 of my own publication already referred to.

Even the contraction of the lamina is not a firmly established characteristic. I have fragments of fronds of two plants, from Vanikoro (Santa Cruz Islands), which show some pinnae of typical enough *Platytaenia* and others of equally typical *T. blechnoides.* Such material leaves more doubt as to the specific than as to the generic status of the plant. Reports of its occurrence in the Philippines and Singapore are more than possibly due to local variants of *T. blechnoides.*

Such local variation in the direction of *Syngramma pinnata* is responsible for *Taenitis interrupta,* described from Singapore. But in Fiji the plant representing *S. pinnata* is constantly of this character—the sori broken up into longer or shorter fragments, and these

not rarely tending to occupy one longitudinal line on each side of the costa.

24132. **Syngramma**, J. Smith, London Jour. Bot., 4:166, pls. 7–8, 1846.

The first species in Smith's enumeration is *Syngramma vittaeformis,* which will best be accepted as the type of the genus; its type is Cuming No. 329, from Samar. The discussion preceding the list of species dealt chiefly with *S. alismifolia,* which Christensen accepted as the type; but the plant discussed was stipulated as *not Diplazium alismifolium* Pr., which clouds both name and type if that plant be chosen. The genus includes sixteen recognized Oriental species; one from America has been referred to it. It includes several sections which have received generic names, but they are closely related, whatever their status. The simple frond not being a primitive form, *S. pinnata* may be regarded as the oldest form of *Syngramme,* the genus thus being cognate with *Taenitis* or derived from the latter. If, further, all of these ferns having presumably an indusiate ancestry, this be sought in *Schizoloma,* the loss of indusium occurring with or without a concomitant withdrawal of the sorus from the margin, then *Taenitis,* with its longitudinal fertile commisure is the more primitive, and *Syngramma* is derived from it, by a breaking up and rearrangement of the fertile area. This would seem far-fetched if it were all conjecture, but we have before us the steps in the unstable Fijian form of *S. pinnata.*

24133. **Craspedodictyum** Copeland, Phil. Jour. Sci., 6:84, 1911.

The type of the genus is the Papuan *Craspedodictyum grande.* A genus of five known species (see Phil. Jour. Sci., 38:147, 1929), best developed in New Guinea, and extending to Sumatra and the New Hebrides. It is an obvious relative of *Syngramma,* in which it was included while only one species was recognized, but from which it is distinguished by palmate design of frond and by differences in venation and sori. The actual connection with *Syngramma* is not as well known as that of *Taenitis,* and the difference in habit is more conspicuous.

24134. **Hemionitis** Linnaeus.

If this genus dated back only to the Species Plantarum, 1753, as it is commonly cited, the name would apply better to the ferns we call *Antrophyum,* as the first species there cited is now referred to that

genus. *Hemionitis,* however, dates properly from Corollarium Generum Plantarum, 1737, and is based on earlier reports of *H. palmata,* which is accordingly the type. There are several other American species, and a single one, *H. arifolia,* in the Orient, from India to the Philippines. I find no reason to doubt the generic identity of this species and the American type. The discontinuous distribution testifies to considerable antiquity.

I have sometimes regarded this fern as Tectarid, moved by its superficial resemblance to other dimorphic, rosette-forming ferns (*Hemigramma, Stenosemia*) with which it commonly grows, but am satisfied that Diels, following J. Smith, did better in grouping it with *Gymnogramme* and, less immediately, with *Syngramma.* The venation is reticulate but without free included veinlets; the indument is of hairs, which shade into very thin and narrow scales, quite unlike those of *Tectaria,* and the rhizome, while very short, so that the fronds are densely clustered, is typically (but not always) prostrate.

24135. **Gymnopteris** Bernhardi, Schrader's Jour. 1: 297, 1799.

The type is *Gymnopteris rufa,* described from Jamaica. Three Chinese species, with densely hairy fronds, have been placed in this genus; also two Australian species which have scaly fronds. Not having seen the last two, I leave them in place, but the scales justify a suspicion as to the propriety of so doing.

The affinity of *Gymnopteris* and *Hemionitis* has been noted repeatedly and is clear enough.

24136. **Aspleniopsis** Mettenius, *in* Kuhn, Festschrift . . . . Kgl. Realshule zu Berlin (1882), 324.

The genus is monotypic, based on *Gymnogramme decipiens* Mett. The type of species and genus is Vieillard No. 1648, in the Berlin Herbarium, collected in New Caledonia. The species is apparently common in New Caledonia, and reported from New Ireland and the New Hebrides.

Superficially, it resembles the group of *Asplenium unilaterale* so strongly that it is not easy to escape the idea that it is an exindusiate *Asplenium.* However, the clothing of the rhizome with (reddish) hairs and its closed bundle (solenostele), both noted by Kuhn in his generic diagnosis, mark it unmistakably as Dennstaedtiid. In this group it may best be associated with the other genera with elongate sori, and thus construed as related to the apparently most primitive of them, *Syngramma.*

2413x. **Pityrogramma** Link, Handb. Gewächs, 3:19, 1833 (cited from Maxon); Maxon, Cont. Nat. Herb., 17:173, 1913.

The type is *Pityrogramma chrysophylla. P. calomelanos* is almost everywhere in the tropics, and beyond them. We have to deal here with a representative of a large, essentially American group of ferns, which it has been usual to bunch in a "genus, *Gymnogramma,*" defined by the extension of naked sori along the veins, and making no pretense of naturalness. To bring these ferns into such order as is now possible with most of the Oriental ferns, the first task is the recognition of the natural genera. Maxon has made important progress in this in recent years, and only one with his comprehensive knowledge of the species has any chance of doing it correctly.

2413x. **Anogramme** Link (1841).

The type is *Anogramme leptophylla,* known here and there in lands not too cold. Eight other species, widely separated geographically, are recognized by Christensen. Because of the indefinite extension of the sporangia along the veins, *Anogramme* is classed with *Pityrogramme* and other Gymnogrammitoid ferns, but its place is not at all fixed.

2420. **Leptolepia** "Mett. *in* Kuhn, Chaetopterides (1882), 348"; Diels, Nat. Pflanzenfam. I 4:212, 1899.

The type is *Leptolepia Novae-zelandiae,* as this was the first species listed by Kuhn, and its citation is the only reason for regarding the genus as published at that time. Kuhn illustrated the genus by figures of a different species, which is here referred to *Oenotrichia.*

L. Novae-zelandiae is related to that element in *Dennstaedtia* to which are related also such derived genera as *Hypolepis* and *Paesia.* Its stipe is deciduously bristly and permanently rough; its rachises, naked and polished. The frond is somewhat deltoid, and the pinnae, except near the apex, are likewise broad. It is four or five times pinnatifid with narrow, acute ultimate segments. The sori are subterminal on teeth whose apices may or may not be deflexed for the partial protection of the sori. The indusia are free, as to their sides. Typically, the base is attached transversely to the vein, and commonly recurves slightly on both sides, having a form familiar in *Dryopteris* and *Humata;* but toward the apices of the pinnules most of the sori become oblique, descending along the acroscopic side of the vein, the indusium assuming the form typical of *Athyrium,* and sometimes even failing to cross the apex of the vein.

It is probably best to maintain a genus thus typified. The type species, well known in New Zealand, is reported from Queensland. I have also (from Yabim, German New Guinea, collected by Zahn and sent me by Christ) a specimen determined as *Davallia Novae-zelandiae,* but better to be treated as an undescribed species of the same genus.

A genus thus typified cannot include ferns with similar indusia but in all other respects belonging to *Microlepia;* such species have accordingly been segregated, as *Oenotrichia.*

2421. **Hypolepis** Bernhardi (Schrader's Neues Jour., 1^2:34, 1806).

This genus was founded on *Lonchitis tenuifolia* Forst., which ranges from China to New Zealand. The thirty-nine species admitted by Christensen include several incorrectly placed here by other authors. The range is throughout the tropics and beyond them, a large majority of the species being American. The affinity to *Dennstaedtia* is very close, some species differing from typical *Dennstaedtia* species solely in the want of the indusium. *Hypolepis tenuifolia* "is so close to *Dennstaedtia scandens* that if *Dennstaedtia* were not already one of the primitive genera which it is at best hard to diagnose, this plant could be included in it." (From Elmer's Leaflets, 3:825, 1910.)

Within this genus *Hypolepis* are species with the sorus withdrawn from the margins, the modification of the margin, to protect it, naturally disappearing. Such species have been confused with *Dryopteris,* but should be easily placed by their trichomes and stelar structures.

In America, *Hypolepis* may well represent a part of the phyletic line leading to two essentially American groups of genera. The species called *Gymnogramma myriophylla* retains the characteristic general aspects of *Hypolepis* and has the elongate sori of the group of genera formerly bunched as *Gymnogramme.* The species known now as *Hypolepis* and again as *Cheilanthes californica* may not properly belong in either genus; but, with a group of relatives, combines their features in a manner strongly suggesting a line of descent for *Cheilanthes* and its relatives.

24211. **Paesia** St. Hilaire (1833).

The type species is *Paesia viscosa,* an American species. There are nine recognized species, in the tropics of both hemispheres and farther south. It is a very natural genus, but of manifest affinity to that element in *Dennstaedtia* which is construed as representing the parent of *Hypolepis.* To this parent, *Paesia* is as close as is *Hypo-*

lepis, the two daughter genera being cognate. The resemblance of all three groups is so close that some of the native peoples of Mindanao, who are close to nature and very commonly have a native name for each species of plant, use one name in application to the three species, *P. rugosula, D. scandens,* and *H. tenuifolia,* but distinguish the Microlepioid element of *Dennstaedtia* by another name.

24212. **Pteridium** (Gleditsch) Kuhn.

This generic name, published in 1760, remained for more than a century without a species to validate it. The name was used twice in a subgeneric sense, for Algae, in the interim, but not for a genus as such. The type is *Pteridium aquilinum;* if it were not now fairly generally agreed that this is so, I would regard this species as the type of *Pteris.* The genus is usually treated as comprising one species, which is, then, the commonest and most widely dispersed species of fern. The diversity of form and pubescence would justify recognition of many species if there were open gaps between the races.

The affinity to *Paesia, Hypolepis,* and *Dennstaedtia* is altogether obvious.

24213. **Histiopteris** (Agardh) J. Smith, Historia Fil. (1875), 294.

The type is the pantropic and southern species, *Histiopteris incisa.* At least four other species are properly distinguishable, all in the Old World. The general rule that a genus most probably originated where it is found best developed is inapplicable in this case, because all except the type species are presumably local derivatives of it. The distribution of *H. incisa,* like that of *Blechnum capense, Eugleichenia, et al.,* indicates migration northward from the Antarctic Continent. It may be of far southern origin or may have reached that continent from a region more constantly suited to ferns; in the latter event, the probable source was South America, since that region has seen the best evolution of the Hypolepid group as a whole.

Histiopteris is clearly a relative of *Hypolepis,* but much nearer than that genus to *Pteris.* The genus of closest affinity to *Histiopteris* is *Lonchitis* of South America and Africa. *Histiopteris* is a natural group, characterized, along with the features marking the group, by very large, smooth fronds, of indefinite growth in length. The pinnae are sessile, with basal pinnules having the aspect of stipules, present in all species except the Fijian *H. sinuata.* In correlation with the considerable size of the pinnules, the venation is usually reticulate. The stout rhizomes bear scales of considerable width but with others

intermediate between these and hairs typical of the Chaetopterid genera; and on long, slender rhizomes the only trichomes are these typical hairs.

24214. **Pteris** Linnaeus.

As a type species, Underwood elected *Pteris arborea* and Christensen *P. longifolia.* Both are American. The genus includes nearly one hundred and fifty currently recognized species, in all warm lands, all terrestrial. The presence in both hemispheres of a number of groups of related species marks this as an old, as well as a large genus. While clearly enough a member of the group in which it is here included, *Pteris* is as natural a genus as *Adiantum,* and in some respects more errant. Its stems are typically scaly and always short; and with their shortening, and the congestion of the leaves, the vascular system has necessarily changed from solenostelic to dictyostelic. Its nearest more primitive relatives are *Lonchitis* and *Histiopteris.* Without seeing Rosenstock's *Hemipteris,* I do not know sufficient reason for its generic separation; the difference in position of sorus is by no means the chief reason for keeping *Pteris* and *Lonchitis* separate. The *Pteris* species with anastomosing veins cannot be made into a separate genus without the sacrifice of naturalness nor without inconvenience as well.

242141. **Coniogramme** Fée, Genera Fil. (1850–52), 167, pl. 14, *b.*

The type is *Coniogramme javanica,* widespread in the Orient.

A recent monograph by Hieronymus, Hedwigia, 57:266, 1916, admits seventeen species, ranging from Africa to Hawaii; and Maxon adds one from Mexico. Hieronymus finds the center of distribution in the Himalaya-Yunnan region, and regards the genus as very close to *Syngramma.* This opinion as to the affinity has been that of his predecessors from Presl to Diels, but rested on hardly any evidence except the form of the sori. The absence of redness laid it open to suspicion, and the presence of paleae instead of hairs is contrary evidence stronger than anything in its favor. The stelar structure is equally incompatable with near affinity to *Syngramma.* Hieronymus investigated it in two species and found plural "steles," i.e., a dictyostele. This probably depends upon the conditions, not being even a specific character. In exceptionally long rhizomes, a solenostele is still present, but it is more usual for two or more foliar gaps to overlap. In paleae, color, and stelar structure the resemblance to *Pteris* is unmistakable. If, now, one will compare *C. fraxinea* with some

Pteris of similar form—*P. insignis,* or *P. pellucida,* or even *P. cretica*—the similarity in various respects, and particularly in the very characteristic hydothodes, will almost force conviction that the affinity is real and not very remote. It is much more evident than the affinity of *Acrostichum* to *Pteris.*

242142. **Acrostichum** Linnaeus.

The type agreed upon is *Acrostichum aureum.* As one species, or a few, very near together, it occurs in brackish swamps in all warm countries. Recent investigators have agreed in construing it as Pterid. It is a rather isolated fern, whatever its affinity, and my acceptance of this location is tentative.

24215. **Schizostege** Hillebrand, Flora of Hawaii (1888), 631.

The type is *Schizostege Lydgatei,* endemic in Hawaii. To this genus are ascribed two Mindanao ferns, apparently distinct but known only from a single locality. The validity of the generic name is open to question because of the older moss genus *Schizostega.*

Christ (Geographie der Farne, p. 227, and in correspondence) regarded this as a link between *Pteris* and *Cheilanthes,* and I formerly followed him. I am now of the opinion that the affinity is exclusively to *Pteris,* from which it differs in the breaking up and remarkable thickness of the sorus. The paleae, in particular, are those of *Pteris,* and the stoutness of the whole plant points in the same direction. The distribution appears remarkable; but if the genus were represented on a dozen islands along the long line of communication between Mindanao and Maui, by species as rare and local as those now known, it would be more likely than not to have been overlooked. The time is not approached when "discontinuous distribution" over this vast area proves anything except our imperfect knowledge.

24221. **Cheilanthes** Swartz, Syn. Fil. (1806), 126.

Type, *Cheilanthes micropteris* Sw., tropical American.

24222. **Notholaena** R. Brown, Prod. Fl. Nov. Holl. (1810), 145.

Type, either *Notholaena distans* or *N. Marantae* (which are not congeneric).

24223. **Pellaea** Link (1841).

Type, *Pellaea atropurpurea,* North American.

24224. **Doryopteris** J. Smith, Hooker's Jour. Bot., 3:404, 1841; 4:162, 1841.

Type, preferably *Doryopteris ludens* of the Philippines.

These four genera, as it is usual to construe them, are all characteristically American, with comparatively few species in the Orient. A considerable number of related, smaller genera are exclusively American. Acquaintance with the Oriental representatives does not give a true idea of the real affinities within this group, wherefore no attempt is made here to trace them. Collectively, they are construed as probably traceable to *Hypolepis.*

Aside from the fact that the Oriental representatives of this group are regarded as outlying forms, presumably derived from those in America, another difficulty is that the first three genera, as usually construed, are certainly not natural. Both in America and in the Orient, the currently accepted generic distinctions break up the phyletic groups and result in genera which would have no other merit, even if they were convenient. *Notholaena hirsuta* and *Cheilanthes tenuifolia,* the two of these ferns most widespread in the Orient, are congeneric, and belong with *N. distans;* which last is the most eligible type species of *Notholaena,* the prior mention of *Acrostichum Marantae* being purely incidental. Unless the generic lines are very comprehensively drawn, they are not congeneric with the large group of Oriental species represented by *Cheilanthes farinosa.*[8]

24225. **Onychium** Kaulfuss, Enum. Fil. (1824), 144.

The type is *Onychium auratum,* regarded now as a synonym of *O. siliculosum,* a common Oriental fern. A genus of not more than six species, of which one or two are American.

24226. **Cryptogramma** R. Brown (1823).

Type, *Cryptogramma acrostichoides,* of cold North America. A genus of four species, two of which occur in Asia.

24227. **Actiniopteris** Link (1841).

Type and only species, *Actiniopteris australis,* known from Africa to Burma.

The foregoing genera are clearly defined, and not themselves characteristically American. But they are parts of the great, typically American group including the preceding four genera, and are therefore passed over without further discussion.

---

[8] *Cheilanthes farinosa* properly typifies Fée's genus *Aleuritopteris,* Genera (1850–52), 153. This genus should probably be revived. It seems decidedly more distinct from *Cheilanthes* than does *Notholaena*—which has been reduced to *Cheilanthes* by Domin, Bibl. Bot. 85[1] (1915), 133.

2422x. **Neurosoria** Mett., *in* Kuhn. Bot. Zeit. (1869), 437.

Based on *Acrostichum pteroides,* an Australian fern, too little known to be placed with any confidence. The short-creeping rhizome bears narrow scales. The black, polished stipe is common in both the *Cheilanthes* and the *Gymnopteris* groups. I have seen only one sheet of specimens, loaned from Kew, and without dissection could not evaluate the protective margin and gymnogrammitoid fructification as evidences of affinity.

2423. **Cheilanthopsis** Hieronymus, Notizbl. Bot. Gart. Berlin, 7, No. 69 (1920), 406.

The type species is *Cheilanthes straminea* Brause, which may best be called *Cheilanthopsis straminea* Hieronymus, although the combination of names was not formally made in the publication of the genus. Formal distinctions from *Cheilanthes* emphasized by Hieronymus are presented by the bilateral (instead of tetrahedral) spores, and the subterminal position of the sori on the veins. The gross appearance is utterly different from that of any Oriental *Cheilanthes.* There is equally little gross resemblance to *Hypolepis,* to which Hieronymus believed it nearly related. I leave it in this position only because I do not know where it ought to be placed.

243. **Adiantum** Linnaeus, Genera Pl. (1737), 322.

The name was taken by Linnaeus from Tournefort, and the genus is properly typified by the common European *Adiantum Capillus-Veneris.* About two hundred and twenty species are now recognized in all parts of the world, but all terrestrial. Its membership in the great group of Dicksoniid ferns is clear, but it has no proved affinity to any of the minor groups of genera. In form of frond, its range is very like that of *Lindsaya* and *Sphenomeris,* and it particularly resembles the former in the characteristic dimidiate pinnae or pinnules of many species, but this resemblance is not sufficient to prove near affinity. In protection of the sorus, it is superficially like *Hypolepis, Pteris,* and *Cheilanthes,* but it differs more essentially from these and all other genera with reflexed margins in that the reflexed margin bears the sporangia. The probable real affinity is to what are called the Gymnogrammitid ferns, a group much better developed in America than in the Orient, but it is evidently not very close in any one genus of these.

30. **Oleandra** Cavanilles, Ann. Hist. Natural, 1 (1799) : 115.

The type species is *Oleandra neri(i)formis,* described from the Philippines, the type of which is presumably in Madrid. Because the genus as a whole is conspicuously natural (it is sometimes described as the only shrubby fern) and because the original description of this species comprised only what are now recognized as generic characters, specimens from every part of the tropics have been referred to this species. Since several Philippine species conform to Cavanilles' description, nothing but comparison with his type can show which one is true *O. neriiformis,* and whether or not it is local. About two dozen species are now recognized, and this number will increase. They occur throughout the tropics, the species fairly divided between the hemispheres.

The affinity of *Oleandra* and genera immediately to follow, the "Davallieae" in a restricted sense, is clear beyond reasonable doubt.

The connection with any series of genera which can be traced back to comparatively primitive ferns is still to be established; and while this remains true I am treating *Oleandra* and its relatives as a group coordinate with the greater ones of better understood origin. Sometimes excluding *Oleandra,* the usage has been to include these genera with those of Dennstaedtioid ancestry, and the genus *Davallia* has been made to include many of the latter. One reason for this has been similarity of form of indusium, which I regard as of no significance whatever. The stelar structure (dictyostelic in *Oleandra* and its relatives) and the trichomes make any near connection between these groups hard to imagine. It is to be noted that the sorus is not marginal in any member of the *Oleandra* group; it is commonly so misdescribed in *Davallia,* but the only approximately marginal thing about it is the apex of a long indusium. In these respects and in the common epiphytic habit, the resemblance is to the Matonid series; but the indusium bars belief in any near affinity.

Within this group, *Oleandra* is the only genus represented in America. *Davallia* occupies the whole width of the Old World tropics, and the other genera are more restricted in range. On this ground alone, *Oleandra* appears the oldest genus; for the others are quite certainly not representatives of more widespread ancestors. *Oleandra,* however, is a highly specialized, not at all primitive genus. These matters are discussed more fully in a recent paper in the Philippine Journal of Science (34:239, 1927). Also, *Oleandra* is now being

studied in Professor von Goebel's laboratory, and welcome light on its origin is hoped for.

31. **Araiostegia** Copeland, Phil. Jour. Sci., 34:240, 1927.

The stipulated type species is *Araiostegia hymenophylloides,* which ranges from Asia into Polynesia. Perhaps ten other species are known, the number uncertain because they have been described in a variety of genera. Except the type species, they occupy a limited range in the Yunnan-Himalaya region, with one species in Ceylon and one in Formosa. Except for the homogeneity of the group and the probability that *Oleandra* is older than *Araiostegia,* the latter might be traced with some probability to a Cyatheid source, perhaps through *Cystopteris.* The inclusion of these other species in a genus with *A. hymenophylloides* is possibly a mistake. The far-eastern species mentioned when this genus was published are not its relatives, but are severally referable to *Dryopteris, Oenotrichia,* and *Cystopteris.*

32. **Davallodes** Copeland, Phil. Jour. Sci., 3C:33, 1908; 34:242, 1927.

The type species is *Davallodes hirsutum.* There are about ten recognized species, most abundant in the Philippines, with representatives in New Guinea, Borneo, Java, Sumatra, and (an aberrant one) in India. It is a remarkably uniform group in other respects, but very variable as to the indusium. Because certain species of *Davallodes* suggest a transition to other genera, particularly to *Davallia* and *Araiostegia,* there is some reason to regard it as a central genus in the group. The best present view, however, is that no one of these genera is the parent of the others, but that they have a common source not very remote.

321. **Trogostolon** Copeland, Phil. Jour. Sci., 34:251, 1927.

The type and sole known species is *Trogostolon falcinellus,* known only in the Philippines. A small epiphyte, with scandent, bristly rhizome, deltoid, decompound frond, and indusia free except at the base. It combines the smooth deltoid frond of *Davallia* with other features typical of *Davallodes.*

322. **Leucostegia** Presl, Tent. Pterid. (1836), 94.

The type is *Leucostegia immersa,* described from India and reaching to Celebes. The only other species is *L. pallida,* reported from Borneo, Samoa, and a few intervening places. The two are very much alike except in the indusium. Many species like it in the terms used to describe the indusium, and very different otherwise, have been

referred to *Leucostegia,* making it so unnatural that the situation is not made essentially worse by including it in *Davallia.*

These two species are the largest ferns in the group (though *L. immersa* has dwarf forms). With *Araiostegia* species, they are the only terrestrial ferns in the group. That the terrestrial habit is in this case an acquired one, the ancestry having been epiphytic, is practically proved by the vestigial articulation of the stipe.

323. **Humata** Cavanilles, Descrip. Pl. (1802), 272.

The type is *Humata ophioglossa,* described from Guam, now construed as synonymous with *H. heterophylla,* widespread and common in Polynesia and Malaya. The genus numbers about thirty recognized species, not all very distinct, all small epiphytes with coriaceous fronds, deltoid in most species but not in the type and its near relatives. It differs most conspicuously from *Davallia* to which it is nearly related, in form of indusium, which has the sides free and is broad; also the paleae, while usually broad as in *Davallia,* are not ciliate or but slightly so. The geographic range is from Papua and Melanesia, where the species are most abundant, eastward across Polynesia, westward across Malaya, and northward to Burma and Japan.

324. **Davallia** J. E. Smith (1792).

The type species is *Davallia canariensis,* occupying by itself an area, the Atlantis Islands and western Mediterranean, at the far west of the range of the genus. There are approximately forty species, abundant in Malaya and ranging eastward across Polynesia. It thus occupies a wider range than any other genus of its group (aside from *Oleandra*). This might be evidence of greater age, but may be better explained by its being more perfectly adapted than *Davallodes,* for instance, to epiphytic life, with its consequent danger of exsiccation. It shares some of these adaptations with *Humata,* but protects its sorus better with an indusium attached everywhere except at the apex.

325. **Scyphularia** Fée, Genera Fil. (1852–54), 324.

The type species is *Scyphularia pentaphylla,* described from Java, and of uncertain range. There are at least five species ranging eastward to Fiji. It is distinguished from *Davallia* by the acicular paleae most characteristic of *Davallodes,* and by comparatively undissected fronds. Apparently very perfectly fitted for epiphytic life, it is perhaps the youngest genus of its group.

3x. **Arthropteris** J. Smith *in* Hooker's Fl. Nov. Zeal., 2:43, 1854.

The type species is *Arthropteris tenella.* The number of known species is half a dozen or more, the number uncertain because of their polymorphism. The range is from Juan Fernandez west to Africa, the best development being apparently in the Melanesian-Australian region. The position of the genus is uncertain. Several items of resemblance have led to its association with *Nephrolepis.* It is here located with the Oleandrid ferns, as the only group characterized by articulate stipes and indusiate sori. The species known as *Dryopteris orientalis* is probably an *Arthropteris.*

40. **Matonia** R. Brown, *in* Wallich, Pl. Asiat. Rar., 1:pl. 16, 1829.

The type species is *Matonia pectinata,* known from the Malay Peninsula and reported from Borneo and Sumatra. My Borneo specimens of this genus are too distinct for specific unity with the type. Those from Sumatra are more like those from the peninsula, but not identical. The genus is a surviving remnant of a group once widespread. From this group, the series of genera to follow are believed to be descended. *Matonia* itself and *Phanerosorus* differ from all of them in several respects which are proper to them as comparatively primitive ferns, and in one respect, the presence of an indusium, which is not so easily interpreted in this way. In this respect, these two genera are specialized in distinction to their supposed relatives, and are construed as a small, distinct family by those who prefer this course. The family so constituted is homogeneous and easily defined. Its recognition violates no principle, and involves no inconvenience.

I have ceased to maintain Matoniaceae as a family, because doing so seems to involve too much mental confusion. A long series of studies by Bower and his colleagues has established the probability that the series of genera from *Dipteris* to the end of this enumeration are, as a whole, a great phyletic unit, with almost certain affinity to *Matonia.* The groups and series of genera previously dealt with were characteristically indusiate, and nakedness of sorus was a derived condition almost always associated with diffusion of the sorus. In the series remaining, an indusium is absolutely unknown, and I see no good reason for postulating an indusiate ancestry. As a matter of convenience which has no tolerable alternative—as Professor Bower seems to have found, between his second volume and his third—I include in Polypodiaceae all ferns with straight annulus interrupted by the

pedicel of the sporangium, and enough ferns with different sporangia to make the family homophyletic. If then, Matoniaceae constitute a separate family, it is as a very distinct offshoot of Polypodiaceae. In view of its several comparatively primitive features, this relation is not easy to grasp and keep in mind. Moreover, just as we have spoken of the genera of one great series as Cyatheid, and of another as Dicksoniid, without meaning to imply that *Cyathea* and *Dicksonia* were themselves the ancestors of these genera, but merely because *Cyathea* and *Dicksonia* perpetuate some of the ancestral peculiarities, so, and in the same sense, the genera to follow have been called Matonid ferns. But this convenient expression would be hard to justify if *Matonia* were raised to family rank, as a group derived from Polypodiaceae. Accordingly, without overlooking the isolated position of *Matonia* and *Phanerosorus,* it seems best to treat them, like *Dicksonia,* which is by no means so isolated, as members of the great family embracing all branches of the tree of fern-life, down at least to the common trunk of all the genera here discussed.

401. **Phanerosorus** Copeland, Phil. Jour. Sci., 3*c*: 344, pl. 3, 1909.

Phanerosorus sarmentosa, known only in Borneo and there very local, is the type and only known species. It differs from *Matonia* in general form of frond, which is very characteristic in both, in the balanced dichotomy of the pinnae, and in the position of the sorus, on a plexus of veins in *Matonia,* on a single vein in *Phanerosorus.*

41. **Dipteris** Reinwardt, Sylloge Pl., 2: 3, 1824.

The type is *Dipteris conjugata,* which ranges from southeastern Asia into Polynesia, with considerable range of detail of form. To the north, two moderately distinct species, *D. Wallichii* and *D. chinensis,* are recognized. The other two, more distinct, are *D. quinquefurcata* in Borneo and *D. lobbiana* in and west of Borneo. The plant in northern Luzon determined as *D. conjugata* approaches *D. chinensis.*

D. conjugata is a stand-forming species, in several respects notably suggestive of *Matonia.* It is less primitive than that genus in most of the significant characters, but more so, in my opinion, in being exindusiate. At any rate it is much nearer to the common parent of the many genera now construed as members of the same group. *Dipteris* is an old genus, better regarded as a remnant than as comparatively new because of its restricted range. Although the original generic diagnosis did not distinguish it at all from *Polypodium,* it is really distinct and isolated.

4211. **Christiopteris** Copeland *in* Perkins' Fragmenta Fl. Phil. (1905), 188; Phil. Jour. Sci., 12C: 331, 1917.

The type species is *Christiopteris Sagitta,* known in Luzon and Mindanao, usually an epiphyte. Three others are known; one each in Sikkim, Siam, and New Caledonia. The Himalayan species, *C. tricuspis,* a terrestrial fern, has received the most thorough study, by Bower, but all are better known than are the species of most genera. The affinity to *Cheiropleuria* is fairly close. That to *Dipteris* and *Matonia* is unmistakable, but not so close. And there are characters in common with *Hymenolepis* and *Photinopteris* and to other genera, and to species of *Phymatodes,* which must be construed as inheritances in common; but the tracing of the lines of evolution through which these various apparently independent characteristics have been preserved in their various combinations has not been accomplished.

The most invariable marks of the group are elongate stems with reticulate bundles, exindusiate sori, reniform or bilateral spores, and paleae with peltate bases. In genetic correlation with the dictyostele is the reticulate venation of the frond, except where the dissection of the latter limits the expression of this tendency. Secondary characteristics are a secondary vascular system for the fertile areas, articulate stipes, dichotomous branching of the frond, a specialized hypodermis under the upper epidermis of the frond, peltate scales and paraphyses, and other peculiar paleae.

The group is essentially Oriental.

4212. **Cheiropleuria** Presl, Epim. Bot. (1849), 189.

The type species is *Cheiropleuria bicuspis,* described from Java. It is regarded as including all plants in the genus; the known range is north to the Liu Kiu Islands and east to New Guinea. Exemplifying the danger exposed in the introduction, it has been made into a proposed monotypic family; on the other hand, the affinity to *Christiopteris* is well established. It is usually terrestrial but has been reported as an epiphyte (Epim. Bot., *loc. cit.*).

4213. **Hymenolepis** Kaulfuss, Enum. Fil. (1824), 146.

The type is *Hymenolepis spicata,* for which *H. ophioglossoides* was improperly substituted by the author of the genus. Its range is from Madagascar, across Polynesia. *H. platyrhynchos* is a very distinct species, in the Philippines and Celebes, remarkable for the protection of the fruiting area by the broad, reflexed, but motile margin. Several less distinct species are recognized. With its simple frond and sharply

differentiated fertile apical segment, the genus is most distinct in appearance from any other. It has still to be studied as thoroughly as *Christiopteris,* but the special vascular supply of the hymenium, and the paraphyses, justify placing it near *Christiopteris.*

4214. **Neocheiropteris** Christ, Bull. Soc. bot. France, 52 Mém. I (1905), 21, as new name of *Cheiropteris* Christ, Bull. Boiss. 6:876, 1898.

The type is *N. palmatopedata* Christ, from Yunnan; no other species is known. It is a rather isolated fern, but most nearly related to *Christiopteris,* particularly to *C. varians.* The frond is thin and without any trace of the peculiar foliar hypodermis of *Phymatodes.* The sorus is borne on a thick parenchymatous pad, with a deep but not double vascular tissue. Paraphyses are present; and some protection is afforded the very large sori by a border of small, armed paleae.

4221. **Platycerium** Desvaux, Mém. Linn. Soc., 6:213, 1927.

The type is *Platycerium alcicorne,* originally described from Madagascar. The genus includes about sixteen accepted species, more abundant in the Old World, but with a few in America. The genus combines some rather primitive features with a very high specialization of the fronds, which makes it one of the most distinct genera in the family.

As to its name, there has been a valiant attempt to establish *Alcicornium* as preferable to *Platycerium.* The former, as a name, dates from the preceding year; but, as I translate the passage, it reads: ". . . . this is *Acrostichum alcicorne,* or at least a species or variety of the genus (*Alcicornium*) which one will not fail to make of these plants after they shall be better studied." (Gaudichaud, *in* Freycinet, Voyage autour du Monde, 1825, p. 48.) Before the realization of the condition for making the genus, or with its realization, Desvaux published *Platycerium,* which Gaudichaud very properly accepted. The future tense is no fit medium for publication with a fixed date.

4222. **Cyclophorus** Desvaux (1811).

The type species is *Cyclophorus adnascens,* a coastal epiphyte, widespread in the Orient, described from Malabar. Nearly one hundred Oriental species are known. Two Ecuador species are referred to it, one of which is the type of J. Smith's genus *Niphidium.* This

is an unusually distinct and natural genus, which received from Giesenhagen a model of monographic treatment—"Die Farngattung Niphobolus (1901). Its stellate trichomes indicate affinity to *Platycerium,* and the hypodermis of many species is similar to that of *"Phymatodes."* Of all fern genera, it is most highly specialized anatomically in fitness for epiphytic life, as its relative, *Platycerium,* is, by gross morphological modification of the frond.

4223. **Drymoglossum** Presl, Tent. Pterid. (1836), 227.

The type was *Drymoglossum piloselloides,* now known as *D. heterophyllum,* from India and Malaya. A dozen other species, including three in the American tropics, are recognized. Christensen has been engaged recently in a study of these species and his publication may be awaited for information as to the limits and affinities of the genera represented.

4224. **Elaphoglossum** Schott (1834).

The type species is *Elaphoglossum conforme,* described from St. Helena and accredited to most tropical regions. As construed of late, this is a genus of almost four hundred accepted species, common throughout the tropics but most numerous in America. The small, aberrant groups in America and St. Helena, although nearly related, would better be restored to generic status, in order to leave so large a group as homogeneous and uniform as possible. It will then *look like* a natural genus, characterized by simple fronds and acrostichoid fructification. It will not, however, *be* a natural genus. The majority of the Oriental species are relatives of *Cyclophorus,* and it is given its location here on that ground. *E. aemulum* (Kaulf.) Brack., an Hawaiian species, is probably Blechnid (see Bernice P. Bishop Museum Bull. 59 : 14, 1929), and I mistrust that still other strains are represented in the "genus" as it is at present defined.

423. **Polypodium** Linnaeus.

The type species is *Polypodium vulgare,* a very common fern of the North Temperate Zone, reported also from South Africa and New Zealand. The genus has been commonly construed as including all ferns with naked, round or roundish sori and articulate stipes, and sometimes far more broadly still. As construed here, it includes such species with free veins, clearly and nearly related species with veins anastomosing in the manner of *Goniophlebium* but without pinnae jointed to the rachis, and a large number of tropical species in both hemi-

spheres which, with shortening of the rhizome and decrease in size of frond, have more or less completely lost the articulation of the stipe. I do not try to decide whether or not the tropical American ferns hitherto placed in *Goniophlebium* as a subgenus should be left in *Polypodium.* The same is true of other groups not represented in the Orient—*Campyloneuron, Pleopeltis,* etc. Without any of these, and without the aberrant free-veined groups which follow—*Grammitis, Calymmodon, Acrosorus,* and *Prosaptia*—all of which have names in *Polypodium,* it remains a genus of more than four hundred species, of which about one hundred and seventy are in the Eastern Hemisphere and Hawaii.

With the recognition of *Matonia* and *Dipteris* as the more primitive representatives of this great group of genera, there is a temptation to regard the free-veined genera (of this group) as in general less primitive than those with anastomosing veins. This temptation is strengthened by the fact that *Christiopteris* and its relatives retain some characters regarded as primitive, which *Polypodium* is regarded as having outgrown, and that there are points of marked resemblance between these genera and *Microsorium.* Whatever evidence there is of this kind is more than outweighed by the fact that, except for one species of *Platycerium,* all of those netted-veined genera are confined to the Old World, and all of the derived or presumably recent genera, as judged by structure, are likewise exclusively Oriental or exclusively American, while not only *Polypodium,* but also one or more of the derived groups with free veins are spread around the world. As to *Dipteris* and *Aglaomorpha* and *Drynaria,* there may be evidence of affinity in the similarity of the venation, and they still occupy the same geographical area. *Matonia* is not in the least like them in venation. And *Phanerosorus* has its veins wholly free except for the anastomosis of two veinlets in the sorus, and even this is not constant.

Any genus *Polypodium* must include *P. vulgare.* Included in the genus will be the relatives of that species, more or less immediate.

As has just been emphasized by Christensen (Dansk. Bot. Arkiv. 5 [1928], No. 22), the nearest relatives of *P. vulgare,* aside from forms so much like it that their specific distinctness is questionable, are species found in both hemispheres along its southern boundary, with veins more or less reticulate in the manner of *Goniophlebium.* Between such species with occasional or irregular anastomosis of veinlets (as in *P. californicum*) and those with a regular row of areolae (as in

P. nipponicum and a group of Chinese species), there is no chance at all of a generic distinction.

The relation between *P. vulgare* and the great group of small tropical epiphytes which might be called *Ctenopteris* is by no means so clear. These may later be recognized as better separated, whether as one genus or as many. Among them are very many species which show no articulation of the stipe, but these form no one phyletic group. Several offshoots of this group are represented among the genera to follow. Other specialized species and groups of species have been so treated; among genera which can be recognized if one so please are: *Lepicystis, Cryptosorus* (which I am more disposed to transfer to *Prosaptia*), *Thylacopteris,* and *Adenophorus. Thymelium* is more probably related to *Grammitis,* in spite of its dissection of frond, and *Holcosorus* to *Microsorium.*

It would obviously be easy to picture *Goniophlebium* as derived from *Polypodium,* and *Microsorium* as derived from *Goniophlebium.* This has apparently been the prevalent view, so far as men have ventured to picture the details of descent in this group; and it may well be correct. I have preferred to regard these groups as cognate, rather than as a series, because of unreadiness to construe *Christiopteris, Platycerium,* and *Elaphoglossum* as derived from *Polypodium,* and the conviction that there is real affinity between *Microsorium* and its apparent derivatives and these genera and *Dipteris.*

4231. **Prosaptia** Presl, Tent. Pterid. (1836), 165.

The type species is *Prosaptia contigua,* the second species listed by Presl, but construed as including the first, a common epiphyte ranging from Ceylon across Polynesia. The sori are deeply immersed in the body of the frond, in cavities which, in *P. contingua,* open toward the margin. All writers since Presl (and he tentatively) who have recognized this as a genus, or as a natural group, have included in it species, like *P. alata,* with similar cavities contiguous to the margin but opening downward rather than laterally. Thus bounded, it is a genus of a scant dozen species. Christensen (Mitth. Inst. Bota. Hamburg, 7:158, 1928), very reasonably extends it to include species with similar cavities which are not marginal; among them *P. obliquata* (Bl.) Mett. Mettenius long ago went farther, including *P. nutans,* a species with less remarkably developed cavities. When construed thus broadly, *Prosaptia* include *Cryptosorus* Fée, of which the species figured by Fée is construed by Christensen as *Polypodium venu-*

losum. Construed as including *Cryptosorus, Prosaptia* becomes a genus of thirty or forty species. But there is nowhere any conspicuous natural break between species with deep cavities and those with shallow cavities, nor between the latter and those with superficial sori. What is more important, species with superficial and with more or less immersed sori occur in more than one minor phyletic group of species, so that it is impossible to use this character by itself as a generic distinction in this great group of species.

It is further true that we know no such connection between any of these tropical epiphytes and *Polypodium vulgare* as we do between *P. obliquata* and *P. contigua.* It would thus seem more reasonable, if we were working with a clean slate, to call all of them *Prosaptia,* rather than *Polypodium.* Of course all of them, including *Prosaptia,* can be called *Polypodium,* as is done by many writers. But the fact remains that *Prosaptia* in its typical development is too different, not only from typical *Polypodium* but also from the great group of species with superficial or nearly superficial sori, for convenient inclusion in one genus. My present course is accordingly to construe it as including only species with extremely immersed sori in or very near the margin.

Prosaptia is not a "genus incertae sedis." Its location has been recognized by every botanist who seriously strove for a natural arrangement, so clearly that it has been rather a "genus incerti status."

4232. **Grammitis** Swartz, Schrad. Jour., 1800[2], 17 (1801); Annals of Botany, 1:430, 1805.

The type should be *Grammitis linearis* Swartz, regarded as identical with *Polypodium gramineum* Sw., a west Indian species.[9] The genus was defined as including ferns with naked, elongate, straight sori. In later usage it is restricted to those with simple, more or less entire fronds and free veins. About eighty species are recognized, in the tropics of both hemispheres, somewhat more numerous in the Orient.

The affinity of *Grammitis* to *Polypodium* § *Ctenopteris* is unmistakable, so clear that it has been usual to treat it also as a section of *Polypodium.* Both groups being old enough to have spread around the world and to develop many minor groups, it is not strange that we are unable to connect them with any certainty by means of really

[9] But Swartz cited, as a synonym, *Asplenium angustifolium* Jacq., now questionably identified with *G. Billardieri* Willd.

intermediate species. We do know many species intermediate in appearance, but there has been ample time for their evolution from either parent. *Ctenopteris* (using the term in a broader sense than the original, to include the great group of tropical *Polypodium* species with more or less pectinate fronds) is probably older than *Grammitis,* and therefore, since they are nearly related, likely to be the parent group. However, for reasons particular to the several groups, I am more disposed to regard the minor and more local phyletic groups intermediate in dissection of frond as derivatives of *Grammitis,* and also to include in *Grammitis,* as Blume did, a number of species with serrate, incised, or somewhat pinnatifid fronds. All *Grammitis* species are small, many of them fairly minute. With smallness of fronds, the value of an elongate rhizome disappears; accordingly, most of the species have the fronds closely clustered. Some species retain articulate stipes, but many show no visible trace of the joint.

42321. **Oreogrammitis** Copeland, Phil. Jour. Sci., 12*c*: 64, 1917.

A monotypic genus, based on *Oreogrammitis Clemensiae,* from the summit of Mount Kinabalu, Borneo, the type of which is in the herbarium of the Bureau of Science, Manila. It is a very small fern, derived from *Grammitis,* with elongate sori, usually uninterrupted on one side of the costa or on both, borne on an anastomosing vein parallel to the costa as in *Blechnum.* It is a product of evolution, parallel to that of *Cochlidium,* but cannot be combined with that genus because the superficial sori, slender stipes, and paleae indicate independent origin in *Grammitis.* For similar reasons, it cannot be combined with *Vaginularia,* to which the resemblance is also wanting.

42322. **Cochlidium** Kaulfuss (Berl. Mag. 5 [1820]), 36 or 303—not seen); Enum. Fil. (1824), 86.

The type species is the American *Cochlidium graminoides. Pleurogramme,* the name by which these ferns have been known when distinguished from *Monogramma,* is a later synonym of *Cochlidium.* Eight or ten species have been recognized as *Pleurogramme,* fairly divided between the hemispheres. The affinity to *Grammitis* has been pointed out repeatedly—see particularly Goebel, Flora, 117: 91, 1924. For the Oriental species of this group, van Alderwerelt set up the genus *Scleroglossum,* but without any clear distinction from *Pleurogramme,* which he apparently confused with *Monogramma.* Goebel's judgment is: "Es scheint mir also derzeit kein entscheidender Grund vorzuliegen,

welcher zu einer generischen Trennung der asiatischen und der amerikanischen Pleurogramme-Arten nötigen könnte." With this I agree, the more readily because the absence of paraphyses is used by van Alderwerelt as a distinctive feature of *Scleroglossum.*

Cochlidium pusillum (Blume) n. comb., *Vittaria pusilla* Blume, Enum. (1828), 199, is the first described and most widespread Oriental species. There are others, but their identity needs to be established before their names are transferred.

42323. **Calymmodon** Presl, Tent. Pterid. (1836), 203.

The type species is *Calymmodon cucullatus, Polypodium cucullatum* Nees et Blume, described from Java, and reported from the mossy forests throughout the Malay region. This is a genus which cannot have a type specimen studied by its author, because Presl drew up his generic diagnosis from a figure by Blume—a figure so strange that van Alderwerelt tried to base another species on it. In a recent monograph (Phil. Jour. Sci., 34:259, 1927), I have recognized twelve species, centered in Malaya and reaching out to Ceylon, Luzon, and Samoa. One more, from Indo-China, has since come in.

The descent may have been from either *Polypodium* or *Grammitis.* Blume regarded the direct affinity as being to *Grammitis,* and I am inclined to agree.

42324. **Acrosorus** Copeland, Phil. Jour. Sci., 1 Suppl. (1906), 158.

The type species is *Acrosorus exaltatus,* of which the type is in the herbarium of the Bureau of Science, Manila. Six species are described, the geographical extremes being Perak and Samoa. It is a genus of the mossy forest. It is like *Prosaptia* in a purely formal conformity to imperfect diagnoses of *Davallia,* unquestionably polypodioid in affinity, but more probably, in my opinion, derived from *Grammitis* than from *Ctenopteris.* The apparent enclosure of the sori is not due to their being immersed, but to the concrescence of the sides of monosoric segments over superficial sori. The same effect would be produced if the sides of the fertile segments of *Calymmodon* grew together. Future collections are likely to make the source of *Acrosorus* clear in detail, but not to connect it directly with *Prosaptia* or *Calymmodon.*

42325. **Loxogramme** Presl, Tent. Pterid. (1836), 214; Copeland, Phil. Jour. Sci., 11C:43, 1916.

Anthrophyum § *Loxogramme* Blume, Flora Javae, 2:73, 1828.

We have here another name taken from Blume by Presl, but with less resulting confusion than in the case of *Goniophlebium,* because all of the possible types are congeneric. Blume founded his section on the fern I have renamed *Loxogramme malayana,* which he mistook for *Grammitis lanceolata* Sw., a near relative. The first species cited by Presl is *L. coriacea* = *Grammitis coriacea* Kaulf., a synonym of *L. lanceolata* (Sw.) Presl, the second name listed by Presl. The genus includes more than twenty species, ranging from Africa to New Zealand and north to Japan. There is also a Mexican species which seems to belong here. Of the species listed in Christensen's Index, Suppl. II: 21, 22, 1917, *L. Duclouxii* Christ, *L. Fauriei* Copel., and *L. Makinoi* C. Chr. should be reduced or returned to *L. salicifolia* Makino. *L. scolopendrina* should be distinguished from *L. involuta. L. spatulata* from China has been published more recently. And *Polypodium Dictyopteris* Mett. of New Zealand is transferred to *Loxogramme.*

The genus is manifestly a derivative of *Grammitis,* which with increased stature, has evolved a correlated anastomosis of the veins.

Paltonium Presl, Epim. Bot. (1879), 156.

The type is *Paltonium lanceolatum,* an American fern, probably related to other American polypodioid ferns. Three Oriental species have been referred to this genus; I have seen none of them. Judging by description, *P. vittariiforme* Ros. is referable to *Loxogramme.* The study of the hitherto unnatural *Drymoglossum* group may serve to locate *P. sinense* and *P. novoguineense.*

424. **Goniophlebium** (Blume) Presl, Tent. Pterid (1836), 185, quoad syn.

Polypodium § *Goniophlebium* Bl., Fl. Javae (1828), 132.

Schellolepis J. Smith.

The fixing of a type of *Goniophlebium* presents all of the typical problems arising in such work. As a genus, it was set up by Presl. The first species listed was "*Goniophlebium Haenkei* (*Polypodium attenuatum* Presl)," native of the American tropics. Presl never saw any species listed by Blume. On the ground that a subgenus or section has no formal status, the American type has been accepted by some botanists, and many American species have been named *Goniophlebium.* My judgment is that while a section or subgenus is *à priori* without status, it can acquire one; and that by charging or crediting Blume with responsibility for the name, Presl gave one to Blume's

Goniophlebium; that when he took Blume's name and as much of a definition as Blume had given, and cited Blume as his authority, he necessarily took also Blume's type. I do not regard the two species, or the two groups, in question, as congeneric; *Goniophlebium* is an exclusively Oriental genus, if Blume is responsible for the name.

But this is far from ending the question. Blume's first species, in his discussion and in his plates, is called "*Polypodium cuspidatum* Don." Blume presented a full description and an excellent plate of the fern to which he gave this name. It certainly is not *P. cuspidatum* Don (which is now held to be *P. leiorhizon* Wall.; Mett.). It is the fern known of late as *P. persicifolium* Desv. Here we have three possibilities:

1. The type is that of *P. cuspidatum* Don, as fixed by citation;
2. The type is that of *P. cuspidatum* Blume nec Don;
3. That the type species is *P. persicifolium* Desv., and that therefore the type of that species is the type of the genus.

I dismiss the first and third because they impute to a group of ferns for which we look to Blume for a type, a type which he (1) utterly misunderstood or (3) knew nothing about. The demand of reasonableness is that, as exactly as we can, we fix the type of a genus in accord with the author's concept of it. The genus itself may be a great group of species. It must be typified by one species. Upon this, botanists are now agreed; but the same confusion and possibility of interminable confusion which have gradually brought botanists to this agreement, are coercing us to the realization that a genus, like a species, should have a type specimen; and that when possible the specimen so recognized should be the one on which the author of the genus based his idea of the genus. Unfortunately, in many cases this is impossible, but it is the most reasonable procedure when it can be done.

With the experience of nearly two centuries, with the resulting confusion and uncertainty, it has become an indefensible procedure to set up a genus without a concrete, material basis of its concept. We are constrained to interpret and construe in matters already historical, but should spare our successors, as far as we know how to do so, from any added burden of this kind. Until a competent congress of botanists shall codify rules on this point, it seems safest to cite the specimen most responsible for the idea, as a part of the description of any new genus. If this idea of type specimens be accepted, the type of *Goniophlebium* was Blume's specimen, the subject of plate 82 of

the Flora Javae, of the species we know as *Polypodium persicifolium* Desv., or, better, *Goniophlebium persicifolium* (Desv.) Bedd.

As here construed, going back to Blume's use of the name, *Goniophlebium* is a genus related to *Polypodium* and to more than one section of *Microsorium;* typically epiphytic, with elongate rhizome clothed with attenuate paleae with peltate bases; fronds pinnate, with pinnae articulate to the rachis; veins anastomosing to form single areolae or single rows of areolae between the main veins with one excurrent free vein in each areola; sori terminal on the excurrent veinlets in the costal areolae, rarely in others. About fifteen recognized species, of which one, *G. subauriculatum,* ranges from Asia to Polynesia; the others comparatively local.

There is real affinity to the pinnatifid species with similar venation, occupying an area contiguous and overlapping on the north, and thence around the North Temperate Zone, but I am leaving these in *Polypodium.* I am doing the same, for the present, with the small group of Bornean species, *P. coloratum, P. proavitum,* etc., with pinnatifid or barely pinnate fronds and venation suggestive at once of *Polypodium, Goniophlebium,* and some *Microsorium* with venation simple in correlation with very narrow segments.

425. **Microsorium** Link., Hort. Berol, 2:110, 1833.

The type is *Microsorium irregulare,* an unstable cultivated strain of *Acrostichum punctatum* L., Sp. Fil., ed. 2, 2:1524, 1763, now to be called **Microsorium punctatum**, a very common epiphyte from Africa to Polynesia. A genus of probably two hundred species, confined to the Old World, the center of distribution in the Malay region.

The group of ferns now under discussion is that most familiar, probably, as *Phymatodes,* a name published three years later than *Microsorium,* and originally applied to a different minor group. All of the known species have names in *Polypodium,* and if any of them lack names in *Pleopeltis* it must be by van Alderwerelt's oversight. *Pleopeltis* has a Mexican type with less affinity, in my judgment, to any species of *Microsorium* (or *Phymatodes*) than *Polypodium vulgare* has to some of them. While this has been my opinion for more than two decades, and I have been steadily disposed to dismember the *Polypodium* of Hooker and his followers whenever I could see the way to do this satisfactorily, and have been whittling off aberrant groups, I have left this one, without changing the name of a species except to correct identifications, because I was satisfied of the affinity

of this group to that of *P. vulgare* and because of doubt as to the proper number and size of the fragments.

The time having come for a decision, I propose to recognize a genus comprising the following groups, as listed in Christensen's Index, page L:

b. Microsorium, represented or typified by the type of the genus.

c. Atactosia, by **M. musifolium** (Bl.) = *Polypodium musifolium* Bl., Enum. (1828), 134.

d. Colysis, *partim*, by **M. hemionitideum** (Wall.) = *Polypodium hemionitideum* Wall., *Colysis hemionitideum* Presl, Epim. (1849), 127. Presl's genus *Colysis* included also species of *Selliguea* and of *Loxogramme.*

f. Lepisorus, by **M. lineare** (Thunb.) = *Polypodium lineare* Thunb., Fl. Jap. (1784), 335.

h. Paragramma, by **M. longifolium** (Bl.) = *Grammitis longifolia* Bl., Enum. (1828), 119.

k. Phlebodiopsis, by **M. accedens** (Bl.) = *Polypodium accedens* Bl., Enum. (1828), 121.

l. Microterus, by **M. neglectum** (Bl.) = *Polypodium neglectum* Bl., Enum. (1828), 121.

m. Phymatodes, by **M. Scolopendria** = *Polypodium Scolopendria* Burm., Fl. Indica (1768), 232.

n. Allothecium, by **M. pteropus** (Bl.) = *Polypodium pteropus* Bl., Enum. (1828), 127.

p. Symplecium, by **M. insigne** (Bl.) = *Polypodium insigne* Bl., Enum. (1829), 127.

r. Arthromeris, by **M. wallichianum** (Spr.) = *Polypodium wallichianum* Spr., Syst. Veg. 4 (1827), 53.

s. Phymatopsis, by **M. taeniatum** (Sw.) = *Polypodium taeniatum* Sw., Schrad. Jour. 1800[2], 26; Syn. Fil., 38:232, 1806.

This list is given as the most convenient and understandable way of showing the scope I propose for the genus. The larger part of these "sections" are minor phyletic groups. The genus includes other such groups, and the list of genera which have been proposed for its species would include many not here mentioned. Until the genus can receive a more or less monographic study, my disposition is to abstain from the transfer of species to it, except as publication of them is demanded for other reasons.

Microsorium is the parent group of a considerable number of others, best regarded as genera. It is so rich, in fact, in daughter groups, that Goebel (Ann. Jard. Buit., 39:163, 1928), dealing with only a part of them, was moved to give geometric expression to the situation by abandoning the classic figure of a family tree and substituting a radiation of daughter groups, like the radii of a sphere. Both are figures of speech, and, as trees do not have to fork dichotomously but may as well have whorls of branches, I like better to keep

the old figure; in this instance it falls hardly short of producing a witch's broom.

Some discussion of their connection with *Microsorium* will be presented as these derived genera are taken up, and the source of *Microsorium* is touched upon in the discussion of *Polypodium.*

As here construed, *Microsorium* becomes a genus of ferns related to *Polypodium,* having as group characters the epiphytic habitat, elongate rhizomes with reticulate vascular system and broad paleae, articulate stipes, and exindusiate dorsal sori; and as diagnostic characters, fronds simple, pinnatifid, or rarely pinnate or of other form, irregularly reticulate venation with irregularly oriented and commonly branched free included veinlets, and round or oblong sori; typically distinguished from *Pleopeltis* by an hyaline hypodermis with wavy lateral walls, underlying the upper epidermis of the frond. It includes a considerable number of evident phyletic groups susceptible of generic status, but not at present sufficiently definable to make their recognition as genera expedient.

4251. **Diblemma** J. Smith, Hooker's Jour. Bot. 3:399, 1841, *nomen;* 4:65, 1841.

A monotypic genus, based on *Diblemma samarensis,* the description of which was incorporated into the generic diagnosis. Smith subsequently abandoned this genus—which may be reason enough why others should. It is characterized by strictly marginal sori, interrupted on Samar specimens (Cuming, No. 332 the type; Jagor, No. 953, *Taenitis samarensis* Mett.), but usually continuous on those from Mindanao (Weber, Nos. 1159 and 1493; Elmer, No. 13259). It is an offshoot too distinct for convenient inclusion in *Microsorium,* in spite of the fact that its affinity to the type-group of that genus is clearer and closer than that of the majority of the phyletic groups still included in that genus. Specimens of *D. samarense* sometimes have some sporangia decurrent from the margin along the veins. **Microsorium tenuilore** (J. Sm.; Kze.) = *Drynaria tenuiloris* J. Sm. *nomen; Polypodium tenuilore* Kze. in Mett., *Polypodium* (1857) No. 150, has some of its sori elongate, but most of them round, both forms densely mixed over the surface of the frond, but except for its fructification it is so much like *D. samarensis* that they have been combined as one species. It is also very close to *M. longissimum* Fée (*Polypodium myriocarpum* Mett.), which is likewise not perfectly stable in form of sorus. I use

Fée's name for this species on the ground that *Phymatodes myriocarpa* was not sufficiently published by Presl.

4252. **Leptochilus** Kaulfuss, Enum. Fil. (1824), 147.

The type is *Leptochilus axillaris,* an epiphyte described from Luzon, and known from India to Papua. One other species is described, from Sumatra. It is a derivative of *Microsorium* § *Eumicrosorium,* cognate with *Diblemma.* The fertile frond is narrowly linear, with acrostichoid fructification, and the articulation of the stipe seems to have lost its function. For a more complete discussion, see Phil. Jour. Sci., 37 : 338, 1928.

4253. **Dictymia** J. Smith, Bot. Mag. 72 Comp. (1846), 16; Hist. Fil. (1875), 115.

The type is *Polypodium attenuatum* R. Br. As this specific name is accepted for *P. attenuatum* H.B.W., published in the same year, Brown's fern was renamed *P. Brownii* Wikstr., and, as the type of *Dictymia,* must be **D. Brownii** (Wikstr.). It was already the type of *Dictyopteris* Presl, Tent. Pterid (1836), 194, but that name was first applied to a genus of Algae. *D. Brownii* was described from Australia; it is ascribed to New Zealand, New Caledonia, the New Hebrides, and Fiji. I have seen no specimens from New Zealand and the New Hebrides. There are two species in New Caledonia, one of which is **D. Mettenii** = *Polypodium Mettenii* (Univ. Calif. Publ. Bot., vol. 14, p. 368, 1929). The other New Caledonia species, and the one in Fiji, remain without distinctive specific names.

The convenient diagnostic difference between *Dictymia* and *Microsorium* is provided by the free included veinlets in the areolae of the latter. *Dictymia* is probably one of the many derivatives of *Microsorium,* and more particularly related to the southern group represented by **M. diversifolium** (Willd.) = *Polypodium diversifolium* Willd., Sp. Plant., 5 : 166, 1910. The superficial resemblance to *M. longifolium* (Bl.) is very striking, but that species has two solid layers of hyaline cells under its upper epidermis, the upper one moderately wavy, as is characteristic of *Microsorium,* though not invariably present. *Dictymia* has its mesophyll remarkably uniform from one epidermis to the other, the uppermost layer being slightly flattened and weak in chlorophyll, but otherwise undifferentiated. The series of cell divisions leading to the formation of the stoma is also very different.

4254. **Selliguea** Bory, Dict. Class. Hist. Nat., 6:587, 1824.

The type is *Selliguea Feei,* widespread in Malaya and Papuasia and accredited to Polynesia. About three dozen species have been referred to *Selliguea* as a section of *Polypodium,* these including two from America and perhaps one dozen with thin, divided fronds, doubtfully symphyletic with the type of the genus. Both the coriaceous and the herbaceous groups of species are derived from *Microsorium* § *Colysis.* Whether or not the independence of these groups extends back into *Colysis,* which would demand either their generic separation or the inclusion in *Selliguea* of the common source, will have to be determined by future study. I do not know the supposed American species but suspect them of quite independent origin.

The genus is characterized by the fusion of points and lines of fructification, so as to form a single linear sorus, running obliquely from near the midrib to near the margin, between each pair of adjacent main veins. In other respects, the characters inherited from *Microsorium* are retained.

42541. **Campium** Presl, Tent. Pterid. (1836), 238; Copeland, Phil. Jour. Sci., 37:341, 1929.

The first species listed was *Campium punctulatum,* "*Acrostichum punctulatum* Presl nec Linn." Because it is not practicable to apply that name with confidence to any plant, I have proposed the recognition of *Campium costatum* as the "standard species." As construed in my monograph, *Campium* is a genus of about sixty known species, ranging from Africa to Samoa, characterized by terrestrial habitat, obsolescence of the articulation of the stipe, reticulate venation, free included veinlets which have tended to disappear in the evolution of groups within the genus, and acrostichoid fructification. One group of species, constituting Presl's genus *Dendroglossa,* is cognate with *Selliguea,* derived from *Microsorium* § *Colysis*; if *Campium* as here construed is a thoroughly natural genus, this is its most primitive element. The group of *C. quoyanum,* the largest and most widespread element of the genus, is either derived from *Dendroglossa* or very closely related to it. Still another group of species, including *C. costatum,* with its center of evolution in India but closely related to *C. heteroclitum* and its group of derived species, shows signs of affinity to *Microsorium* § *Arthromeris.* However, until an independent source of these other groups can be established with some such cer-

tainty as the origin of *Dendroglossa* from *Colysis, Campium* will best be construed with its present scope.

4255. **Dendroconche** Copeland, Phil. Jour. Sci., 6*c*:91, 1911.

The type species is *Dendroconche Annabellae* (Forbes), known only from New Guinea. This fern bears orbicular sterile, humus-collecting fronds, and fertile fronds in which the costa of the orbicular base is carried, with a very narrow wing, beyond the apex of the orbicular base, the wing widening again to form the oblanceolate-linear fertile lamina.

It is derived from **Microsorium linguaeforme** (Mett.) = *Polypodium linguaeforme* Mett., Ann. Lugd. Bot., 2:228, 1866, a very variable species of the Moluccas, Papua, and Fiji, and doubtfully present in the Philippines. Intermediate forms between *Dendroconche* and its parent are found in Papua, making it less clearly cut off than are very many of the species of *Microsorium*. It is a genus in process of evolution. Its recognition as a genus is purely for convenience. The inclusion in *Microsorium* of a species with fronds modified as a whole as humus-gatherers would complicate its definition against *Drynaria*. And *Dendroconche* cannot be included in *Drynaria* because its evolution is independent. Also, I like to have a few genera which can be recognized as in the act of evolution, to exemplify the fact that all genera have originated in this manner.

4256. **Aglaomorpha** Schott, Gen. Fil. (1834), pl. 20.

The type species is *Aglaomorpha meyeniana,* a very showy Philippine epiphyte. For reasons to be presented in the discussion of *Drynaria,* I construe this genus so broadly that it becomes very difficult to define. When I defined it less inclusively years ago (Phil. Jour. Bot., 6C:140, 1911) as "Genus . . . . ex affinitate Polypodii (Drynariopsidis) heraclei derivatum," etc., the part of the diagnosis just quoted was its most essential element. Goebel has quoted the entire diagnosis and, ignoring this part of it, said that only the final word, soris "compositis," is new and that it is incorrect. The word is indeed ill chosen, descriptive of what Goebel calls coenosori rather than pleosori, which, as I understood, *A. meyeniana* has. I have now to amend the diagnosis again, inserting after the clause quoted above, "et eam includente," and including species with simple, elongate and enlarged sori, but not with sori transgressing the main veins. The last clause is to exclude *Merinthosorus* and *Photinopteris.* It includes the entire natural group with finely reticulate, prominent venation, abscissile segments, and

humus-collecting bases, except four known specialized derivatives: *Drynaria,* characterized by specialized distinct humus-collecting leaves; *Thayeria,* by specialized branches of the rhizome, each bearing one frond; and *Merinthosorus* and *Photinopteris,* with "sori" which cross the main veins. Included are three known species, *A. pilosa, A. Buchanani,* and *A. Hieronymi,* which, with loss of size, have lost the humus-collecting leaf bases and fleshy rhizomes characteristic of the group as a whole.

The components of *Aglaomorpha* as here construed are:

1. *Drynariopsis.* **Aglaomorpha heraclea** (Kze.) n. comb., *Polypodium heracleum* Kze. Bot. Zeit. (1848), 117. No fern is more worthy of this generic name. Sori simple and almost always punctiform, exceedingly numerous.
2. **Aglaomorpha coronans** (Wall.; Mett.) n. comb., *Polypodium coronans* Wall.; Mett. *Polypodium* (1857) No. 242, pl. 121; Hooker, Sp. Fil. V, 94. Without a subgeneric name, though included in Kunze's section *Symplecium.* Sori elongate and often confluent, in a single row between the main veins, the fertile segments not contracted or but slightly so.
3. *Psygmium. A. meyeniana,* the type of the genus. Sori moderately enlarged, in a single row on each side of exceedingly contracted segments, the upper part of the frond being thus specialized for reproduction.
4. *Dryostachyum. A. splendens* and *A. novoguineensis* (Brause) C. Chr. The sori much enlarged, filling squarish areas separated by the main veins, fertile segments correspondingly broader than in *Psygmium,* but likewise restricted to the apex. *A. pilosa* and *A. Hieronymi* are without humus-collecting bases.
5. *Hemistachyum,* Phil. Jour. Sci., 6C:141, 1911. *A. Brooksii.* Fertile segments still wider and with several much enlarged "sori" between each pair of main veins. Here also probably *Drynaria leporella* Goebel.
6. *Holostachyum,* Phil. Jour. Sci., 9C:8, 1914. *A. Buchanani* and *A. Schlechteri.* Like *Hemistachyum* except that entire fronds instead of portions of fronds are contracted for devotion to reproduction, and the base is not dilated.

Subgenera 1, 2, and 6 are the most susceptible of generic status.

42561. **Drynaria** (Bory, Ann. Sci. Nat., 5:464, 1825).

Described by Bory as a subgenus of *Polypodium, Drynaria* was used in the following year by Gaudichaud indiscriminately as the name of a genus and as some minor group. Thus *Drynaria Gaudichaudii* is discussed under that name on the preceding page, but listed as a synonym of *Polypodium diversifolium* on page 355 of Freycinet's Voyage. *Drynaria* was made a section of *Phymatodes* by Presl. J. Smith, Hooker's Jour. Bot., 4:60, 1841, first raised it unequivocally to generic rank, with *Phymatodes* and *Dipteris* as sections. The type is *D. quercifolia,* a very common Malayan fern, reaching to China and Australia.

In its original and usual (Diels, Christensen) sense, it comprises the group derived from *Microsorium* and characterized by punctiform, or at any rate round, sori, abscissile pinnae or segments, finely reticulate and conspicuous venation, and the formation of special fronds metamorphosed as humus-collectors. As a result of a thorough study of a number of these species and their relatives, Goebel (Ann. Jard. Bot. Buit., 39:117, 1928) now construes it as including ferns otherwise similar but without specialized humus-collecting fronds. Nobody will fail to respect Goebel's judgment, particularly in a matter which has had his interest for more than forty years; and yet, accepting his evidence—mostly in perfect agreement with my own observations but in part correcting me—I cannot draw his conclusions from it. I do not take seriously his objection to the basing of genera on vegetative characters. They distinguish Oomycetes from Siphoneae, and should suffice to distinguish genera if they do for classes. It is true that a large part of the fern genera based on vegetative characters alone have been abandoned. But I know no other distinction between *Sagenia* and *Dryopteris;* and they distinguish *"Phegopteris"* from *Polypodium* to the satisfaction of most pteridologists. One character seems to me as useful as another, if it serves as a mark of a phyletic series or group. Botanists are approaching agreement as to this, and are even paying serious attention to purely physiological characters, imperceptible by us except as they are tested outside the plant—I am thinking of serum reactions as evidences of affinity.

Coming down to the group under consideration, Goebel and I agree on *"Polypodium" heracleum* as a primitive member of it, not necessarily a parent or ancestor, but a species exemplifying the ancestral characteristics. From such a fern, we suppose that there have evolved a considerable number of species, naturally alike in many respects but conspicuously unlike in others. One of these, *Polypodium coronans,* is remarkably different in fructification, having elongate and more or less confluent sori in a single row between the main veins, as in *Selliguea;* except that it usually does (but rarely does not) have a dilated base, it is vegetatively much like *P. heracleum;* the two have never been separated generically.

Another group of derived species is characterized by the suppression of the upper, green portion of a part of the leaves, producing the familiar scale- or humus-collecting leaves of *Drynaria.* I see no reason to doubt that these are a homophyletic group, more nearly related to one another than to *P. heracleum. D. sparsisora* is the species

most like *P. heracleum;* from it a series can be traced, through *D. quercifolia,* to the several species of more limited distribution, with single sori between the main veins. The latter species occur in a belt along the northern edge of the range of the genus, where conditions are unfavorable for the existence of large epiphytes. They are all comparatively small plants, which is clearly correlated with the decrease in number of sori; they also tend to become terrestrial, the scale-leaves dwindling with loss of demand for the performance of their function.[8] These little vestigial scale leaves are inescapable evidence of the descent of these species (*D. descensa, D. Delavayi,* etc.) from *Drynaria* species with fully functional specialized scale leaves.

Likewise from such an ancestor as *P. heracleum,* but surely not from *Drynaria,* with its dimorphous vegetative fronds, are descended a considerable group of species which at first retained the vegetative scheme of *P. heracleum,* with the base of all fronds dilated and scarious, but evolved a specialization of the apex of the frond for the production and ready dissemination of the spores, the modification consisting of a constriction of the lamina and enlargement of the sori. Modified to just this extent, we have *Aglaomorpha meyeniana,* the type of its genus. The next step is the further enlargement of the sori, to such a size that it compels the widening of fertile segments or pinnae. This is the condition of *Dryostachyum splendens,* the type species of *Dryostachyum.* Goebel reduced *Aglaomorpha* to *Drynaria,* but leaves *Dryostachyum* generically separate, a course explicable only by his not having had representative material of *D. splendens.* Because *D. splendens* can be traced backward with strong probability along the line just sketched, while *D. pilosum* is clearly related to it, and has no other likely ancestry, it is reasonably regarded as a species derived from *D. splendens.* It is a much smaller species, with a stipe and without a scarious base, and with a slender rhizome. These changes in form and structure are correlated with the loss of size, the evolution being parallel to that already noted in the smaller species of *Drynaria.*

Goebel will have it that the humus-collecting habit and fleshy rhizomes were not evolved in the "Kampf ums Dasein." Be their origin what it may, they were maintained and fixed in such a struggle; and when, with loss of size or descent to the earth, they are no longer necessary equipment for it, they promptly degenerate and disappear in the *Drynaria* and *Aglaomorpha* groups alike.

---

[8] Christ, Mém. Soc. Bot. Fr., 1: 23, 1906.

Several other peculiar species have evolved from the *Aglaomorpha* group, more probably than from a more primitive source, and certainly not from *Drynaria.* Among these are several New Guinea species, of no great size, in which the fructification of *Dryostachyum* occupies entire fronds with restricted lamina, producing dimorphism of the common type—sterile fronds with ample lamina and fertile fronds only ample enough to produce the sporangia. As these differ from the older species of *Dryostachyum* only in that whole fronds instead of definite parts of the frond are contracted and devoted to spore production, they do not seem to demand generic separation. *Merinthosorus, Photinopteris,* and *Thayeria* are more distinct, and may best be held generically distinct.

Leaving the last three as genera, without more argument, the disposition of the other species of this alliance has been far from agreed upon. They can be regarded as all constituting one genus; Goebel approached this, and might have done it completely if he had really known *Dryostachyum splendens.* Its absence from his material left a gap between *Aglaomorpha* and *D. pilosum.* At the other extreme, *Drynaria, Aglaomorpha,* and *Dryostachyum,* and *Poronema, Drynariopsis* (which might be divided in turn), and *Holostachyum* as well, might all be treated as genera.

I have chosen a course between these extremes. To avoid an excessive number of genera, I construe *Aglaomorpha* broadly, with the inevitable result that it becomes hard to define. There are two reasons for making this the vague genus of the group, if any one is made so in order to restrict the number. The first is that *Aglaomorpha meyeniana* and *Dryostachyum splendens* are more nearly related than are most members of the group, differing only in the degree of extension of the sori. But *D. splendens* may, on the other side, hardly be separated from *D. pilosum* and from *Holostachyum.* By the time a genus includes all of these, it is already hard to define; and it is better to add still other elements to such a group than to spoil the easy definition of another group by making it receive them. *Drynaria,* restricted to species with distinct scale-leaves, is easily defined and recognized, and may well be left so. But *Polypodium heracleum* and *P. coronans* will clearly be more at home somewhere in the Drynarioid group than in *Microsporium.* They can constitute a genus—or two genera; or they can be placed in *Drynaria,* as various writers have done, usually with other more remote relatives; or they can with equal

propriety so far as regards phylogeny, and more propriety as regards the resultant difficulty of definition, be drawn into *Aglaomorpha.*

The other reason for construing *Aglaomorpha* broadly is that it has the oldest generic name in the group. When *A. meyeniana* is treated as congeneric with any others of these ferns, the latter take its generic name. Goebel's proposition, "Drynaria wurde als Gattung (bezw. als Untergattung von Polypodium) aufgestellt von Bory de St. Vincent," contains its own contradiction. *Drynaria* (Bory) J. Smith disappears as a genus when it is made to include *Aglaomorpha.* In drawing *Drynariopsis* into *Aglaomorpha,* I am only giving to its two species the same names they would properly bear if I accepted the generic boundaries chosen by Goebel.

42562. **Thayeria** Copeland, Phil. Jour. Sci., 1 Suppl. (1906), 165; 7C:41, 1912.

The type species is *Thayeria Cornucopia,* known from Mindanao and Luzon. In its fructification it is like *Aglaomorpha meyeniana,* to which its affinity is unmistakable. I have separated it generically from *Aglaomorpha* because it is unique among ferns in its specialization of branches of the rhizome as parts of the most perfect known humus-collecting structures. This procedure is strictly parallel to the recognition of *Drynaria* as a genus because of the specialization of its humus-collecting fronds, and has evidently not given undue emphasis to the remarkable character of *Thayeria,* since the publication of descriptions in Latin and English, of drawings, and of a photograph have not succeeded in making it credible. Even in his summary of accomplishments in this field, Goebel (Ann. Jard. Buit., 39:227, 1928) includes: "Einer Prüfung bedarf die Organbildung der als 'Thayeria' bezeichneten Drynaria-Gruppe, namentlich die Frage, ob die Blätter hier wirklich nur an Kurztrieben stehen."

Because it exhibits this peculiarity, I have included in *Thayeria* a New Guinea species, *T. nectarifera,* with distinct humus-collecting and spore-bearing fronds. It seems easier to believe that the differentiation of the fronds has been evolved independently in this species than that the specialization of rhizome branches has been evolved more than once; for we know almost countless instances of the evolution of dimorphism of fronds and only these two species with such rhizome branches. The generic combination of these two is therefore justified by their probable phylogeny. It is perhaps equally true that their separation can be justified by their unlikeness.

42563. **Merinthosorus** Copeland, Phil. Jour. Sci., 6C:92, 1911.

The stipulated type specimen is King No. 288, from Papua, identified as *Merinthosorus drynarioides,* which is reported from Penang and the Solomon Islands. It is like *Aglaomorpha meyeniana* in vegetative aspects and in the restriction of sporangia to the narrow upper pinnae of the frond; unlike it in that the sporangia occupy an uninterrupted line on each side of the costa of each of the fertile pinnae.

42564. **Photinopteris** J. Smith, Hooker's Jour. Bot., 3:403, 1841; 4:155, 1841.

The type and only recognized species is *Photinopteris speciosa,* a striking fern of the Malay region, commonly epiphytic but not rarely terrestrial. In fructification it is like *Merinthosorus,* but the fronds are pinnate and stipitate, not humus-collecting, with comparatively slender, hard, glabrescent, lime-coated rhizomes. The nectaries, borne at the base of the costae of the segments of many members of the group, and of uncertain function, are borne on conspicuous auricles on the stipe and rachis of *Photinopteris.* Vegetatively it is more similar to *Aglaomorpha pilosa* than to any other species, the resemblance being in too many features to permit doubt of near affinity.

4257. **Lecanopteris** Reinwardt (1825); Blume, Enum. (1828), 120.

The type species is *Lecanopteris carnosa,* described from Java, and reported from other islands, reaching perhaps to Luzon. It is a very remarkable fern, with smooth, thick pinnate fronds, the sori immersed in variously reflexed or contorted marginal outgrowths of the pinnae, and the rhizome greatly inflated, hollow, and inhabited by ants. Eight other ill-defined species with these characters may be distinguishable (but I suspect that some of them differ chiefly in the time of day of the collection), the range extending to Formosa.

Lecanopteris is almost certainly a derivative of *Microsorium.* The enlarged and almost invariably immersed sori and the texture of the frond suggest § *Phymatodes* as a more definite ancestral group. There is an approximately intermediate group, Christ's section or subgenus *Myrmecophila,* likewise with rhizomes which become hollow, but with the sori placed as in *Phymatodes,* and mostly with persistently scaly rhizomes. The affinity of this group to *Lecanopteris* is absolutely clear; that to any group in *Microsorium,* not equally so. Therefore, as well as because *Myrmecophila* would be a very aberrant group in *Microsorium,* it should either be made a genus or transferred to

Lecanopteris. Since the position of the sori is the only constant distinction, and is more apparent than important, the best course is to construe *Lecanopteris* as including *Myrmecophila.* This combination has already been proposed by van Alderwerelt, but executed in the wrong direction; i.e., by transfer of *Lecanopteris* to *Myrmecophila* as a section, first of *Polypodium* and then of *Pleopeltis.*

The species to be transferred to *Lecanopteris* are:

Probably *not Polypodium leiorhizum.* If this is really a *Myrmecophila,* the group is not derived from *Phymatodes.*

L. lomarioides (J. Sm.; Kze.), n. comb.

Polypodium lomarioides Kze. *in* Mett. *Polypodium* (1857), No. 192. The frond is like that of typical *Lecanopteris* except for the position of the sori; rhizome elongate, scaly.

L. sinuosa (Wall.; Hooker) n. comb.

Polypodium sinuosum Wall.; Hooker, Sp. Fil. 5:61, 1863. The commonest and most widespread species in the group. Fronds simple and sinuate or entire, rarely lobed; rhizome elongate and scaly. A Papuan plant ascribed to this species has a glabrescent rhizome with the frond-bearing branches notably enlarged.

L. Sarcopus (De Vr. et Teysm.) n. comb.

Polypodium Sarcopus De V. et Teysm., *in* Baker, Syn. Fil. (1874), 514. Frond as in *L. lomarioides;* rhizome exceedingly inflated, but scaly like that of *L. sinuosa.* Described from Celebes and reported from China.

L. mirabile (C. Chr.) n. comb.

Polypodium mirabile C. Chr., Index (1906), 545.

Polypodium imbricatum Karsten, Ann. Jard. Buit., 12:168, 1895. Similar to *L. Sarcopus* except that the inflated rhizome is nearly naked, bearing some hairs in place of the scales of the latter species. Known only from Amboyna.

426. **Phlebodium** J. Smith, Hooker's Jour. Bot., 4:58, 1841.

The type species is *Phlebodium aureum,* a common fern in tropical America. Its mention here is due to a report of its collection in Australia (Müeller, Fragmenta Phyt. Austral., 5:128, 1866). Bentham most reasonably questioned the report.

51. **Antrophyum** Kaulfuss, Enum. Fil. (1824), 197.

The first species listed was *Antrophyum pumilum, Hemionitis immersa* Bory, with a new name; the species is known, as *A. immersum,* from the Mascarenes, where described, and the Malay region. Benedict

(Bull. Torr. Bot. Club, 34:445, 1907) selects *A. reticulatum* as the type species. More than forty species are recognized in the tropics of both hemispheres. The American species as a whole are phyletic minor groups distinct from the Oriental. The specific status of the Oriental species is not clear because they are ill defined by macroscopic characters and only in part described in greater detail.

With *Antrophyum,* we take up a distinct and, so far as present knowledge shows, isolated group of genera, the Vittarieae. Like the Oleandrid ferns, these are given a distinct first figure because I do not know how to connect them with any one of the three great groups of genera. It may be expected, however, that in both instances such a relation will be established. In spite of their striking peculiarities, it is altogether unlikely that the Vittarieae constitute a really coordinate group, i.e., that their phyletic separation from other groups is equally remote.

As to relationship within the group, I follow Goebel (Flora, 117:91, 1924) in regarding *Antrophyum* as probably the most primitive member, and *Monogramma* as an extremely simplified derivative. Benedict (Bull. Torr. Bot. Club, 38:153, 1911) has construed the simplicity of *Monogramma* as primitive.

52. **Vittaria** Smith, Mém. Acad. Turin, 5:413, 1793.

The type is *Vittaria lineata, Pteris lineata* L., described from the West Indies, common in America, and sometimes construed as pantropic. Seventy-five or more species are recognized; they occur in all warm lands. As in the case of *Antrophyum,* and for the same reason, they are hard to distinguish by the published descriptions.

53. **Vaginularia** Fée (1843); Genera Fil. (1850–52), 97; Goebel, Flora, 117:110, 1924.

The type is *Vaginularia trichoidea,* described from Cuming's Philippine collection. The commonest species is *V. paradoxa,* known from Ceylon across Polynesia. Others listed by Goebel are *V. subfalcata* and *V. emarginata.* They are all Oriental. *Vaginularia* is distinguished from *Monogramma* by bearing the sori on a lateral nerve, not on the costa; also, its paraphyses are not capitate and the stomata are cut off from the upper end of an epidermal cell.

54. **Monogramma** Schkuhr, Krypt. Gewächse (1809), 82, pl. 87.

The type is *Monogramma graminea,* described from Bourbon and known from the neighboring islands. The only other species left in

the genus by Goebel is *M. dareicarpa,* of the Philippines, Borneo, and New Guinea. They are the smallest Polypodiaceae and the simplest in structure, being veinless except for the costa.

The foregoing enumeration lists and numbers one hundred and thirty-six genera. With the consistent application of approximately the same standards of phyletic and formal distinctness which I have observed in most of the work, the number would be perhaps one hundred and fifty, and few if any new names would be required. When the boundaries of the phyletic groups can be recognized more clearly than I can see them as yet, it certainly will be advisable to break up the group herein called *Microsorium;* this probably will be found true of *Dryopteris* and *Polypodium,* possibly of *Asplenium* and *Cyathea.* It is true, as has been noted, of *Drymoglossum.*

It is not to be anticipated that men will judge the same evidence in exactly the same way. With increase of knowledge, as new species are discovered and old ones are more perfectly studied, our judgment as to what genera should be recognized inevitably changes. For these reasons, we cannot expect, nor even desire, our nomenclature to become rigidly fixed.

We can, and should demand of ourselves that we do, put an end to all confusion and instability which has its origin solely in descriptive pteridography. This becomes approximately possible with recognition of the fact that real genera are natural groups, and with acceptance of the principles that a genus must have a type species, and a species a type specimen. Our nomenclature will be insured against disturbances on historic grounds when we adopt the corollary principle that a genus must have a type specimen and then fix upon the specimens which typify the described genera.

Polypodium is the genus which includes *Polypodium vulgare.* To just the extent to which that species requires a type specimen to fix its nature and insure its stability, so does the genus. The propriety of including any other particular species in this genus must be determined primarily by its affinity to *P. vulgare.* Knowing the species which we regard as so nearly related to it that they ought to be included in the same genus, we formulate a generic diagnosis—that is, a collective definition of them—designed to include these and to exclude all other species. This definition is simply of things as they are seen; and this fact is not altered in the least by the other fact

that the world at large will next use the definition as its means of deciding what species belong in the genus.

The genus exists in nature. It exists just as truly as does a family of men. The family is real if it consists of two parents; equally so if it consists of two parents and their children; of these and the children's children; or if it includes cousins of some more remote assigned degree of consanguinity. Its naturalness is, must be, independent of the limits we assign to it; we may therefore observe our own convenience in assigning these limits. A natural genus may be divisible into two or more natural genera, just as a family is an equally real and natural group if so bounded as to exclude second cousins or to include third cousins. What is necessarily and always true is that the possibility of placing any other given species in the genus with *P. vulgare* is determined by their consanguinity, not by their conformity to a definition.

Pleopeltis angusta H.B.W. typifies the genus *Pleopeltis,* being the only species mentioned when that genus was published. Any genus, except *Polypodium,* which includes that species must be called *Pleopeltis.* The genus *Selliguea* is similarly typified by *S. Feei.* If it suits our convenience so to bound *Polypodium* as to exclude this species, then it and all species treated as congeneric with it must constitute the genus *Selliguea. S. Feei* and *Pleopeltis angusta* cannot be combined in one genus, *Pleopeltis,* unless they are more nearly related to each other than to *P. vulgare,* which does not appear to be the case. If it suits us so to bound our genera that *Polypodium punctatum* (L.) Swtz. and *P. Feei* (Bory) Mett. are excluded from *Polypodium* but left in a genus together, that genus must be *Selliguea.* They can be treated in this way because they are more nearly related to each other than to *P. vulgare.* If it pleases us to separate these two species generically, then *P. punctatum* and every species placed in the genus with it must be called *Microsorium.* Comparing the last two genera, *Microsorium* is probably the parent group from which *Selliguea* evolved; still, if their affinity and resemblance are deemed close and complete enough to demand their union, their name must be *Selliguea. Phymatodes* is more familiar as a generic name than is *Microsorium.* So is *Drynaria.* But if the type of either of these genera is treated as congeneric with *Microsorium punctatum,* it must take that generic name; I have so treated *Phymatodes* but not *Drynaria.*

This enumeration of cases is to illustrate the facts:

1. That affinity, not the terms of a definition, must determine what plants can be united generically.

2. That, the bounds of a genus being determined by our convenience, subject always to the primary demand for phyletic unity, the name of the genus is determined by the almost automatic application of recognized rules; it is the first valid generic name ever given to any plant in the genus. The number of genera ever proposed among the ferns is not so great that the task of determining the type of each, and listing them in the order of publication presents any great difficulty. Let a reasonable rule for determining the type of a genus be formulated and applied, and all confusion and shifting of names on historic grounds might well be at an end within a very few years.

It is only with the recognition of genera as natural groups of related species, in distinction to groups composed essentially of species which look alike or conform to a definition, that agreement upon types can result in real stability. This treatise has been devoted primarily to the demonstration of the fact that this point of view is susceptible of strict and consistent application. With very few likely exceptions, the genera herein presented are truly natural groups. A large majority of them are defined, confidently, in terms of their natural affinity. This is the kind of definition which really identifies a genus. Chiefly as an indication of the reasons for assuming affinity, I have mentioned the conspicuous features by which many of the genera can be recognized. On the whole, however, I have abstained from enumerating marks of recognition, in order to emphasize the basic fact that no diagnosis can have a value, as the essential element of a generic definition, equal to that of a responsible, properly substantiated statement of origin and affinity.

There may be today no other group of organisms of equal size and diversity in which the affinities of the component species and genera are as well understood as they are in the Polypodiaceae. I know no other great group of plants in which so wide a range of characters has been used in this kind of study. The extent itself of our present knowledge makes them a most inviting field for further investigation; it is by further study of the field best known that we draw most interest on our wealth of information. It is in the nature of the case that next year's study will modify my picture of fern evolution; if this were not so, the study would not be inviting. But, whatever

changes may presently be justified in the scope, the names, and the location of the genera I have recognized, the basic principles of this study will stand fast:

1. The genera dealt with exist in nature.

2. They are comprehensible, and therefore definable, in terms of their phylogeny.

3. The effectiveness of the study of systematic botany is measurable by the resulting comprehension of phylogeny.

A NEW CALIFORNIAN SPECIES OF SPHAEROCARPUS

TOGETHER WITH AN ANNOTATED LIST OF THE SPECIMENS OF SPHAEROCARPUS IN THE MANCHESTER MUSEUM, THE UNIVERSITY OF MANCHESTER

BY

GRACE WIGGLESWORTH

University of California Publications in Botany
Volume 16, No. 3, pp. 129–137, 10 figures in text
Issued December 20, 1929

University of California Press
Berkeley, California

Cambridge University Press
London, England

A NEW CALIFORNIAN SPECIES OF SPHAEROCARPUS

TOGETHER WITH AN ANNOTATED LIST OF THE SPECIMENS OF SPHAEROCARPUS IN THE MANCHESTER MUSEUM, THE UNIVERSITY OF MANCHESTER

BY

GRACE WIGGLESWORTH*

Among some Hepaticae collected in California by Miss K. M. Drew was a small *Sphaerocarpus* intermingled with a tuberous species of *Anthoceros,* probably *Anthoceros phymatodes.* Although there was only a small quantity of the *Sphaerocarpus,* male and female plants were present in various stages, from young plants such as the one shown in figure 4 to older plants with ripe capsules (fig. 1). The spore-tetrad markings showed that this was an undescribed species; moreover, the structure of the thallus revealed it to be of more than usual interest.

An attempt was made to obtain some living material for a more detailed study of the developmental morphology, but failing this, it is thought that a short description of the species from the material already at hand, may be useful. Some modification of this description may be necessary when specimens from other localities become available.

Sphaerocarpus Drewei sp. nov.

Plants dioecious about 1–2 mm. long, male plants as large as female. Thallus lobed, simple, with several growing-points, or bifurcate; obliquely growing, with numerous rhizoids on the under side; 4–5 cells thick in the central region, becoming thinner near the margin where leaf-like lobes one cell thick are found. The leaf-like lobes are obliquely inserted, succubous, suberect and decurrent for the greater part of their length. Branches occur with a more distinct axis bearing succubous leaves, especially in connection with the male plants.

---

* Assistant Keeper (Botany) The Manchester Museum, The University of Manchester.

Female plants suborbicular, sometimes with an elongated upturned branch; pale green becoming tinged with purplish-red at the margins of the leaf-lobes and on the exposed parts of the involucres. Average length 1.3 mm., axis .385 mm. wide with cells averaging $88\mu \times 39\mu$; leaf lobes wedge-shaped, average breadth .54 mm., antical side about the same, postical side slightly longer; suberect, marginal cells usually quadrate; $22–33\mu \times 22–33\mu$. Involucres crowded on the axis-part of the thallus; subcylindrical or obovate, average length .997 mm., about half as wide in their broadest part; orifice surrounded by about twelve cells averaging $49\mu \times 30\mu$; median cells $55–110\mu \times 22–44\mu$.

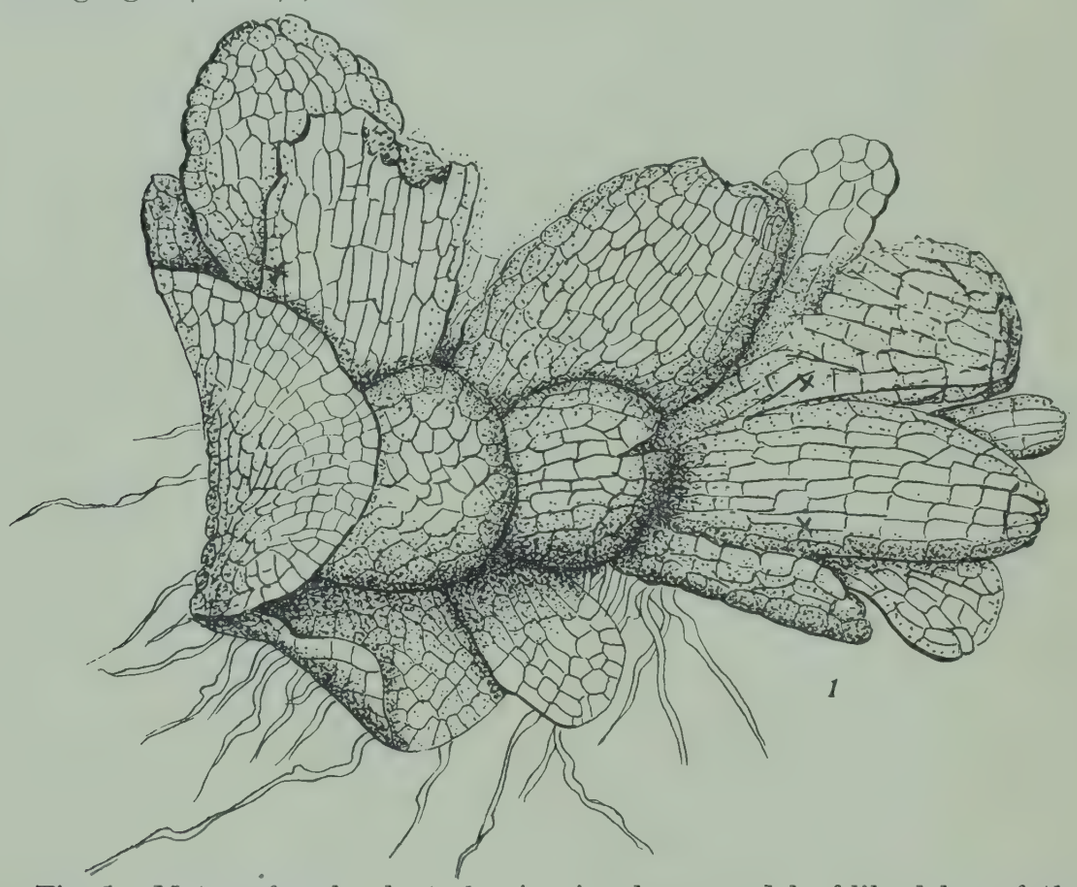


Fig. 1. Mature female plant showing involucres and leaf-like lobes of the thallus. *x* denotes the position of the growing-points on the thallus below the perianths. × 58.

Male plants purplish-red, thallus usually once bifurcate; average length 1.4 mm.; axes .199–.332 mm. wide, with cells $68\mu \times 24\mu$; leaf-lobes as in female plants but rather smaller (average breadth .37 mm.) marginal cells $39.6\mu \times 39.6\mu$. Flask-shaped involucres (averaging .359 mm. long and .066 mm.–.146 mm. wide) cover the dorsal surface of the axis; orifice cells average $55\mu \times 27.6\mu$.

Capsule.—34–59 mm. in diameter; seta very short $33–44\mu \times 66\mu$; foot bulbous, remaining imbedded in the thallus. Spores remaining in tetrads (dark brown, $66–154\mu$ in diameter, lamellate. The lamellae (becoming thickened and granulate) radiate from the outer face of the spores where they are lobed; they thus form more or less parallel lines on the tetrad, branching and anastomosing, but never forming regular alveoli. Sterile cells irregularly shaped, mostly oval; average size $44\mu \times 33\mu$.

Locality.—La Jolla, California. On bare ground, on a hillside near Scripps Institution, associated with *Anthoceros phymatodes* (Drew, 1926).

Two species of *Sphaerocarpus,* occurring in California, have already been described—*S. texanus* Austin (including *S. californicus* Aust., which is now considered to be the same species) and *S. cristatus* Howe. The species described above constitutes a third. According to

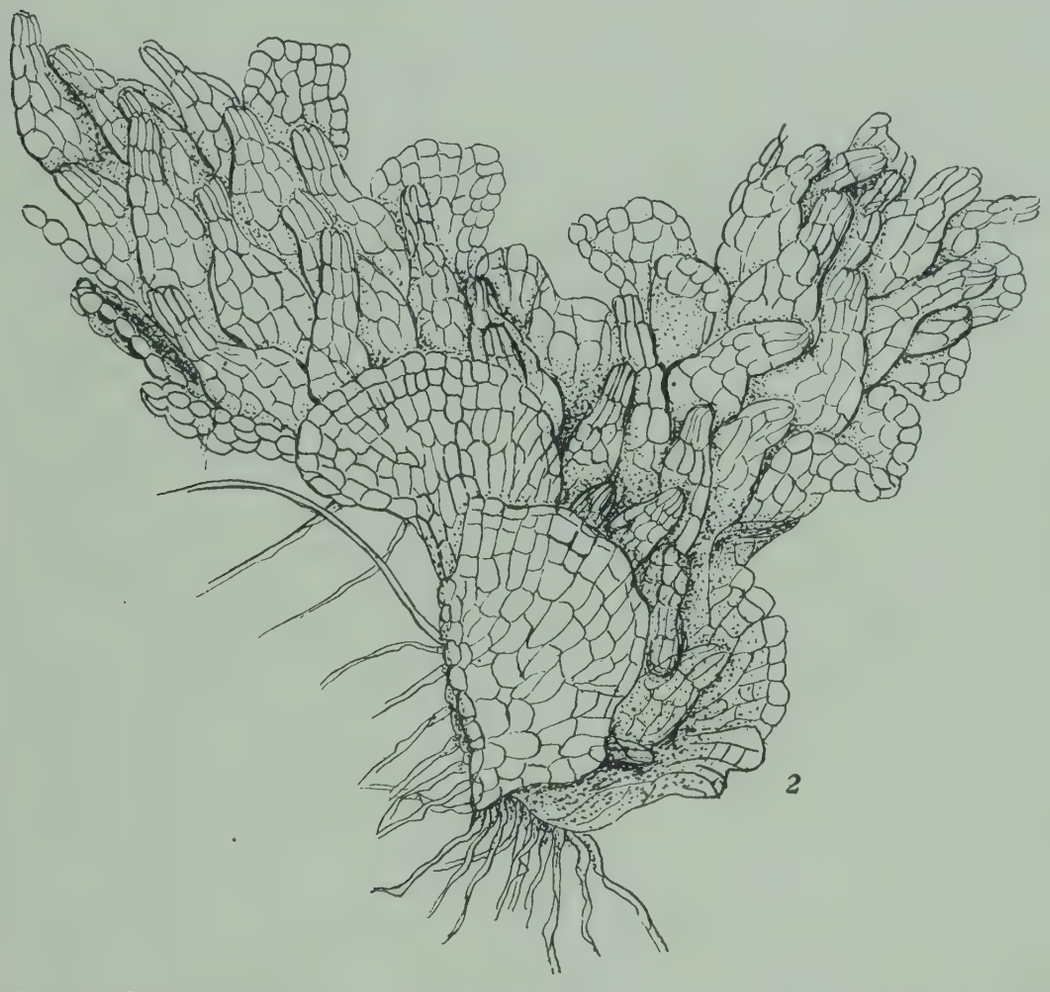


Fig. 2. Mature male plant showing bifurcation of the thallus. The leaf-like nature of the lobes is shown, the multistratiose median part being covered with antheridial involucres. × 58.

Miss Haynes, who made a revision of the genus *Sphaerocarpus* with illustrations of the species (Bull. Torrey Bot. Club, vol. 37, pp. 215–230, pls. 25–32, 1910) there are six species of *Sphaerocarpus* known, four of which occur in North America, two in Europe, and one in South America. With the exception of *S. cristatus,* the spores or spore-tetrads of all these species have areolate markings. *S. Drewei* like *S. cristatus* has lamellate spores but, whereas the lamellae in *S. cristatus* form thin sinuous plates or crests, those in *S. Drewei* form thickened ridges which are more or less parallel (see fig. 9). More-

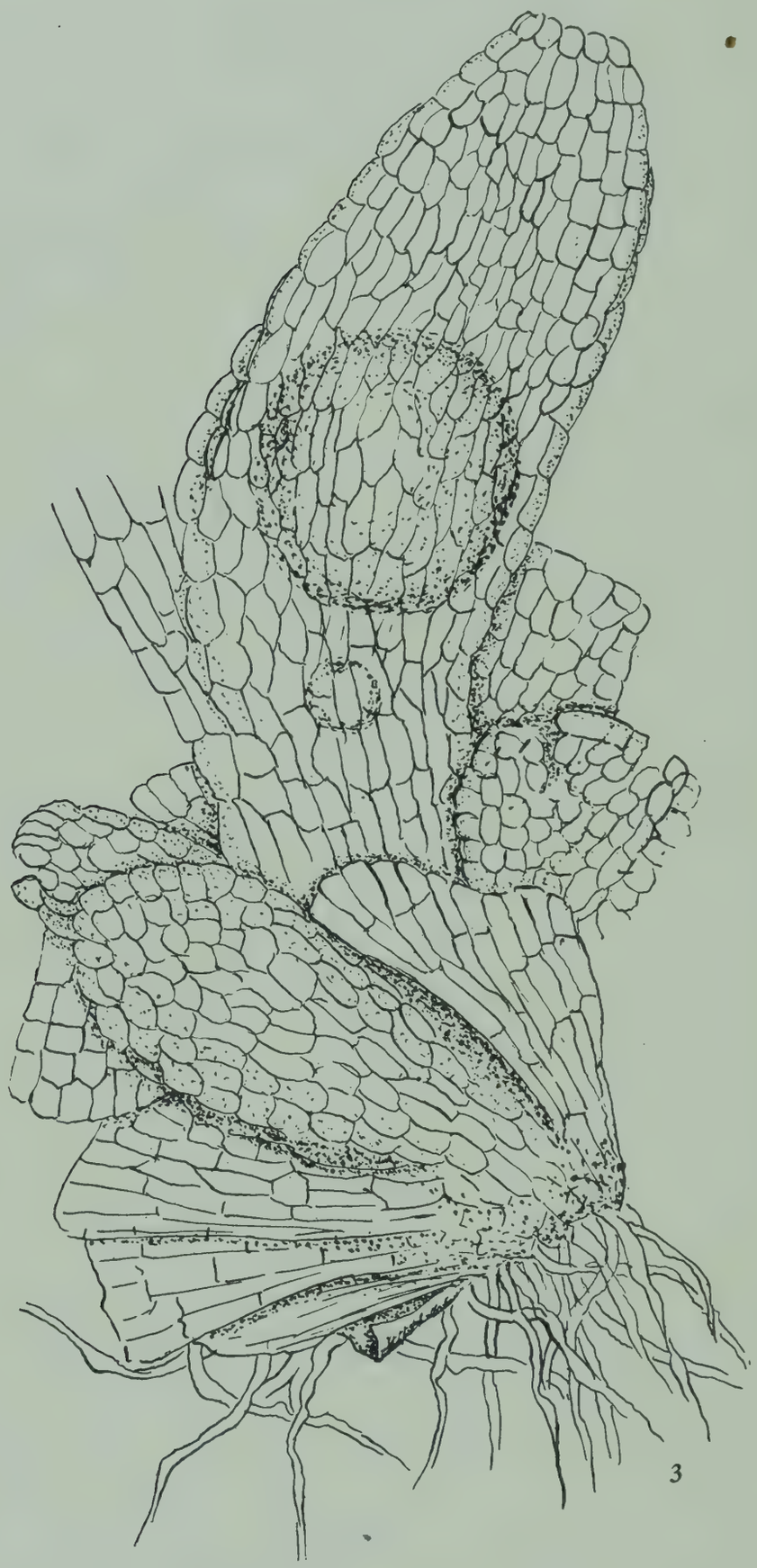


Fig. 3. A female plant with a young sporogonium enclosed in an involucre. × 85.

over, the spores remain in tetrads in *S. Drewei,* while in *S. cristatus* they separate long before the maturity of the capsule. Another point of difference between these two species concerns the behavior of the bulbous foot. This remains imbedded in the thallus when the capsule is detached in *S. Drewei,* while in the case of *S. cristatus* it accompanies the capsule when this is detached from the thallus.

The thallus of *Sphaerocarpus* is described as having a multistratiose mid-rib passing gradually into unistratiose lobes. In this new species the lobes appear to be more definitely leaf-like than in the other species described, approaching the condition obtained in some of the *Fossombronias* and in that interesting plant closely allied to *Sphaerocarpus, Geothallus tuberosus,* which was first gathered by Mrs. Brandegee at San Diego not so far from the locality of the plants described above. *Geothallus* is a larger plant with leaves placed more horizontally, and the involucres are confined to a smaller area. Its spores are larger than those of *S. Drewei* and separate at maturity; they are reticulate but only on the inner face, the outer part remaining thick and smooth; while in *S. Drewei* the reticulations occur on the outer surface of the tetrad.

The occurrence of tubers in *Geothallus tuberosus* is an interesting biological feature. Whether this new species of *Sphaerocarpus* is ephemeral or whether it has some means of tiding over the dry season other than by spore-formation, cannot be decided from the material at hand; this was all gathered in January at the time of greatest rainfall, when sexual reproduction was active.

Sphaerocarpus drewei sp. nov.

Diagnosis.—Dioica. Frons simplex vel dichotoma, ad 2 mm. longa, in medio cellulis pluristratis formata et involucris obtecta, lamellis unistratosis, oblique insertis, succubis, suberectis, decurrentibus. Involucra obovata vel subcylindrica apice truncato vel rotundato. Capsula spherica, seta brevissima, bulbo spherico inserta. Sporae- tetraedrae fusco-brunneae, ad 154μ in diam. lamellis crassis lobatis minuteque palillatis radiatim divergentibus ex externa facie, ramosis et anastomosantibus obtectae. Plantae masculae quam feminae non minores. In terra nuda inter *Anthoceros phymatodes* crescit.

Habitat.—La Jolla, California (K. M. Drew).

THE GENUS SPHAEROCARPUS AS REPRESENTED IN THE HERBARIUM OF THE MANCHESTER MUSEUM, THE UNIVERSITY OF MANCHESTER[1]

In 1891 the Manchester Museum acquired Dr. Carrington's herbarium, which included half of Austin's collection of Hepaticae, and ten years later the other half of Austin's Hepaticae was purchased by the Museum from Mr. W. H. Pearson. The Manchester Museum is fortunate, also, in possessing Mr. Pearson's collection of foreign Hepaticae and R. Spruce's own herbarium.

Austin had not marked particular packets as type specimens, so the packets which bear evidence, from the name of the collector and the date, of being the original gathering, must be considered as type specimens in this collection. In some cases Mr. Pearson has marked the packet "Type." In the following list, the localities and collectors' names in connection with American plants are given, together with some notes regarding Austin's plants.

1. **Sphaerocarpus terrestris** (Mich.) Smith Engl. Bot., 1790. British Isles (8), Germany (6), Italy (5). Locality not cited (1), America (9).

The American section includes four packets marked "e coll. Austin," four marked "e coll. Carrington," and one marked "Spruce herb. prop." They are from the following localities: Aikin, S. Carolina (Ravenel, 1876, Ravenel, 1877, Ravenel, 1852); City Point, Virginia (1867); Mississippi (Hall); Florida (No. 61, Hepaticae Americana, Prep. by Underwood and Cooke).

Mature spores were not found in two of the packets; the others all had spores with larger meshes than those commonly found in *S. terrestris.* Miss Haynes considers that this species does not occur in America. She says she has seen no American species which conform strictly to the characters of this plant.

2. **Sphaerocarpus Donnellii** Austin. Torrey Bot. Club., Vol. 6, p. 157. America (15).

Including five packets marked "e coll. Austin" and six "Ex herb. Carrington." One of the former is inscribed "*Sphaerocarpus Don-*

[1] Species numbered according to Species Hepaticarum of Stephani. The number in brackets signifies the number of packets.



Fig. 4. Young female plant seen from the ventral side showing growing-point, mucilage hairs and rhizoids on the axis-part of the lobed thallus. × 85.



Fig. 5. Single antheridial involucre. × 85.

Fig. 6. Two archegonial involucres, one enclosing a young sporogonium, the other with the remains of an unfertilized archegonium. × 85.

Fig. 7. Transverse section of male thallus. × 85.

nellii n. sp. Flo. Feb. 5, '77 leg. J. D. S." and is presumably the type. Other localities and collectors are as follows: Fernandina, 1878; Florida (James); Charleston, S. Carolina, August, 1878; St. Augustine (J. Donnell Smith, March 1, 1877); Jacksonville, Florida (February 5, 1877); Closter; Sanford (Rapp, March, 1917).

3. **Sphaerocarpus Texanus** Austin, Torrey Bot. Club, vol. 6, p. 158. America (4), England (2), France (2), Belgium (1).

In Species Hepaticarum (vol. 1, p. 197), Stephani states that this plant is not in Austin's herbarium in Manchester. This is a mistake and has probably arisen because the packet containing Wright's material from Texas (the type specimen), was labeled *Sphaerocarpus Berterii?* Mont. in ink, the inscription "*Sphaerocarpus texanus* Aust. San Marco, Texas Dr. C. Wright 1849," being written in rather faint pencil.

As Miss Haynes has pointed out, Austin quotes in his Hep. Bor. Am. (tickets of the specimens) No. 138 "*Sphaerocarpus Berterii* Mont. California, Bolander, Bigelow; Texas, Wright." This was published in 1873. In 1877, he describes Wright's specimen from Texas as *Sphaerocarpus texanus*, and in 1879 he describes, as a new species, *S. Berterii* Austin (exsiccata No. 138 from California), giving it the name *Sphaerocarpus californicus.* Miss Haynes considers that Austin was correct in his first interpretation, that is, in regarding the plants from both localities as the same species. The name, *Sphaerocarpus Berterii* Mont., which he used is misleading as the plants thus named by Austin were not the same as the original *S. Berterii Mont.* (*S. Berteroi* Steph. Bull. Herb. Boiss., vol. 7, p. 657, 1899). The latter is a South American plant collected by Berteroi at Quillota in Chile.

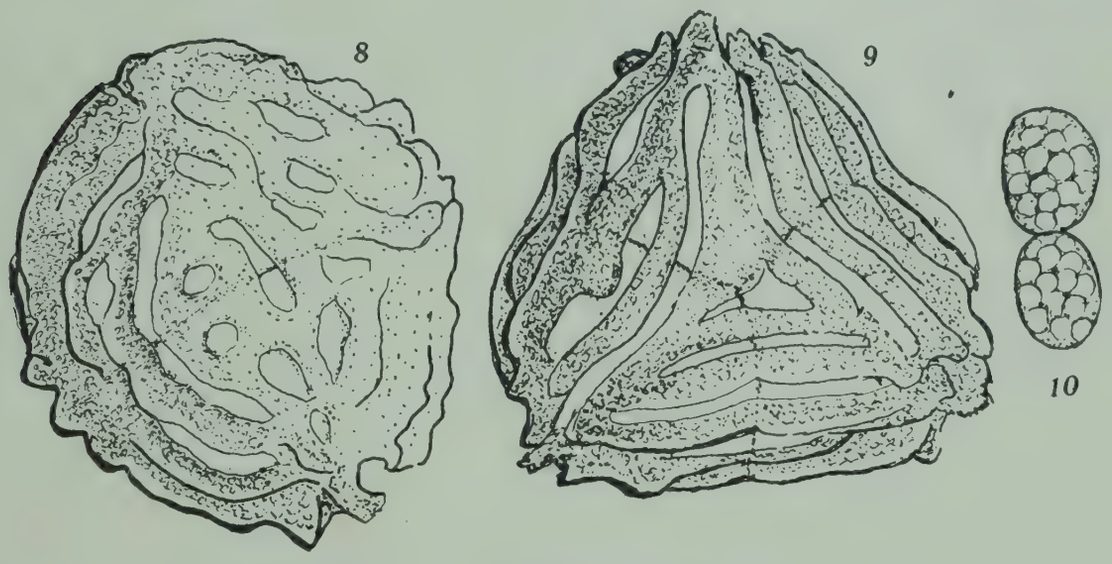
In addition to the type specimen of *S. texanus* in the Manchester Museum, there is a specimen from Sanford S. Rapp (*ex. herb.*), W. H. Pearson, one from Marin County, California (K. M. Drew), and one from Louisiana which was named *S. terrestris* in Spruce herb. prop. The French and Belgian specimens were also included under *S. terrestris,* but these all clearly belong here.

4. **Sphaerocarpus Berteroi** Mont. Stephani in species Hepaticarum, vol. 1, p. 198.

There are no specimens of this species in the Manchester Museum.

5. **Sphaerocarpus Californicus** Austin. Torrey Bot. Club., vol. 6, p. 305.[2] America (3), France (2).

The American specimens include two packets labeled "*Sphaerocarpus Berterii* Coll. Bolander, California" (one labeled "e coll Austin" and one "ex herb Carrington"), which must be considered the type specimens, and one from Mill Valley, Marin County, California. M. A. H. 1896.



Figs. 8, 9. Spore-tetrads. × 450.
Fig. 10. Sterile cells. × 450.

6. **Sphaerocarpus cristatus** Howe. Torrey Bot. Club, vol. 7, p. 66. America (1).

This specimen is from San Mateo County, California, collected in May, 1892, by Dr. D. H. Campbell ("No. 160. *Sphaerocarpus terrestris* Mich. var. *californicus* Aust. Hepaticae Americanae prep. by Underwood and Cooke").

7. **S. Jamesii** Austin. Only the name and locality are recorded by Stephani, Species Hepaticarum vol. 1, p. 198.

There are no specimens under this name in the Austin collection in the Manchester Museum.

There are now two species in addition to those given in Stephani's Species Hepaticarum: *Sphaerocarpus Hians* Haynes, of which there are no specimens in the Manchester Museum, and *Sphaerocarpus Drewei* n. sp., America (1), the specimen described above.

[2] Miss Haynes considers this to be the same species as *S. texanus*, Austin, so there are included here only the type specimen and those specimens with the name *S. californicus* already written on the packet.

ON SOLARIZATION OF LEAVES

BY

RICHARD HOLMAN

University of California Publications in Botany
Volume 16, No. 4, pp. 139–151; 7 figures in text
Issued December 12, 1930

University of California Press
Berkeley, California

Cambridge University Press
London, England

ON SOLARIZATION OF LEAVES

BY
RICHARD HOLMAN

The term solarization as employed in plant physiology refers to a decrease or complete disappearance of starch, following long exposure of leaves to light of an intensity which is, in the earlier hours of the exposure, favorable to abundant starch formation.

On account of the similarity, at least superficially, of the disappearance of starch from leaves after long, intense illumination, to the reversal of the image in photographic plates, Ursprung (1917, p. 57) borrowed the term solarization from photography to designate the phenomenon in leaves, which he first observed.

It was in the course of his study of the distribution of starch, when leaves, previously freed of their starch, were illuminated by brilliant spectra, that Ursprung first observed solarization in plants. In his experiments, light from various sources was concentrated, by means of a large condenser and other lenses, upon a prism or grating. The resulting spectra were projected upon leaves previously freed of starch by being kept for some time in darkness. When the exposures were of short duration, subsequent removal of chlorophyll and treatment with potassium iodide-iodine solution showed maximum starch formation to have taken place in the region of the *B* and *C* lines. When the leaves were exposed for a much longer period, the accumulation of starch extended more and more toward the blue end of the spectrum, but disappearance of starch, partial or complete, took place in the region of the *B* and *C* lines where starch accumulation was greatest during briefer exposures.

Ursprung observed solarization also in attached leaves, starch-free at the beginning of the experiment, which were fixed in a frame and kept approximately perpendicular to the incident sunlight for eight and a half hours. After five and a half hours, a piece cut from the leaf showed abundant starch by the iodine test. That a maximum had, however, already been exceeded was evident from the fact that the

edge of the leaf, which was somewhat shaded by the frame, was much more intensely colored than the unshaded portion. After eight and a half hours little starch remained in the fully illuminated portion of the leaf.

No data as to the intensity of the light falling upon the leaves were supplied by Ursprung, nor were any details given of the "set up" which would make it possible to duplicate, even approximately, the conditions of illumination in his experiments. He said nothing as to the appearance or condition of the illuminated areas of the leaves after the exposures, except that, when the light was too strong the chlorophyll was destroyed and the cells died. But that solarization itself did not necessarily involve the death of the leaf cells was shown by these cells being capable of plasmolysis and deplasmolysis after solarization, and by the fact that, after exposure sufficient to cause solarization, the solarized leaves were able again to form starch, following a period of recovery.

He attributed the disappearance of starch to an inactivation of the chloroplasts, probably connected with strong absorption, high light intensity, and excessive starch accumulation. He suggested also that excessive oxygen production, in connection with photosynthesis, may play a part in this phenomenon, since Pringsheim (1882, p. 340) found that in a mixture of hydrogen and carbon dioxide, or in pure hydrogen the "Lichttod" which he observed, following inactivation by too intensive illumination, did not take place. Ursprung made the further suggestions that, in solarization increased solution of starch may go hand in hand with inhibition of starch formation and that increased temperature, presumably attending intensive solarization, may also favor transformation of starch into soluble substances.

The present paper is a preliminary report on solarization experiments at present being carried on by the author to determine the immediate cause of solarization and the effect of various internal and external conditions upon the phenomenon.

In most of the experiments here reported upon, terminal leaflets of young leaves of scarlet runner bean, *Phaesolus multiflorus,* the same species used by Ursprung, were employed. The light source was a 1,000-watt, 120-volt, "Spotlight" Mazda, mounted on an optical bench, carrying also a plane mirror reflector and a block bearing a glass-walled cooling cell. This cooling cell was kept at constant temperature by a stream of water flowing through it under constant head, and controlled as to rate of flow by a micrometer pinchcock. A silver plate pierced by twelve

rectangular apertures, 11 by 3 mm., was fixed to the glass wall of this cooling cell on the side away from the light. The leaves experimented with were held against this silver plate by means of parallel silk threads. To allow circulation of air between the silver plate and the upper lighted side of the leaf, coarse silver wires were so placed as to prevent the leaf from coming in direct contact with the silver plate. Comparison of the distribution of stomata on the two sides of the leaf showed that more than ten times as many stomata occur on the lower as on the upper side, so that serious reduction of the carbon dioxide supply to the leaf would not have resulted even if the silver wires had not been used.

The apparatus was so constructed that, by means of two sliding shutters within the cooling cell, the twelve openings in the silver plate could be opened one after the other, exposing successive rectangular areas of the leaf surface for various periods. The light intensities used were from 60,000 to 160,000 lux, as measured by the Macbeth illuminometer. It will be recalled that 1 lux equals about $\frac{1}{11}$ of a foot candle, for 1 foot candle is the equivalent of 10.76 lux. Although the intensity of sunlight of a clear day is commonly estimated at about 100,000 lux, Boysen-Jensen (1929, p. 499) has recently published values for sunlight up to 125,000 lux. The light intensities used in my experiments have therefore ranged from about one-half that of maximum sunlight up to values considerably in excess of full sunlight. It should be borne in mind that the light of the tungsten lamp is considerably richer in longer wave lengths, presumably the most effective in solarization, and poorer in shorter wave lengths, than is sunlight.

Comparisons of the results secured with excised leaves and with leaves still attached to the plant showed no difference, either in the rate of starch formation (with short exposures or lower light intensities) or in the rate of solarization. This was perhaps to be expected inasmuch as so small a proportion of the whole leaf surface was illuminated in my experiments. All the unilluminated part of the leaf, about 75 per cent to 80 per cent, was presumably available as a reservoir into which soluble photosynthate might diffuse. Accordingly, most of the experiments were performed with excised leaves. This made it possible to enclose the leaf within a gas chamber fastened against the glass wall of the cooling cell on the side away from the light. Through this gas chamber there flowed a current of air drawn from outside the laboratory. Before passing into the gas chamber the air was brought

to approximately the same temperature as that of the cooling cell by passing it through a copper worm immersed in the latter. The air passed through the gas chamber at such a rate as to preclude all possibility of the supply of carbon dioxide to the leaf being insufficient.

Figure 1 shows the appearance of a leaflet in an experiment in which the light intensity (75,000 lux) and exposures (1 to 12 hours) were insufficient to cause solarization. Starch formation, distinctly

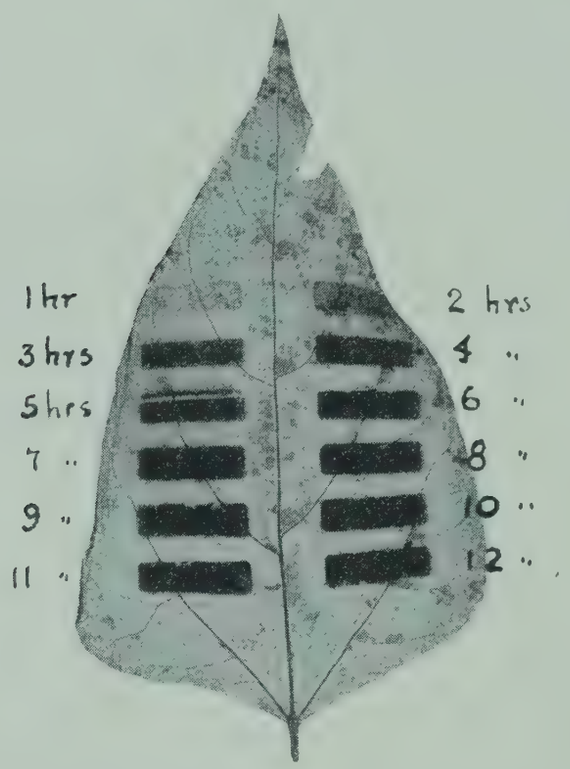


Fig. 1. Leaflet of *Phaseolus multiflorus* freed of starch and then treated with iodine solution after illumination of the twelve areas shown. The duration of illumination is given opposite each exposed area. Temperature 23–25° C. Light intensity about 75,000 lux.

evident after one hour's exposure, increased up to about five hours, this maximum being maintained up to twelve hours when the experiment ended. It should be noted in the case of this leaflet that in each area the starch is uniformly distributed, at least that there is no darker margin surrounding the exposed areas such as appears in solarized leaves. Several of the illuminated areas of this leaf were, before the chlorophyll was removed, of distinctly lighter green color than the unexposed parts of the leaf, a fact to which we shall later refer.

The white line across one of the exposed areas (5-hour exposure) is a shadow of one of the silver wires accidentally misplaced and not observed until the opening of the shutter uncovered this aperture.

In the leaflet shown in figure 2 various degrees of solarization may be observed. The light intensity in this case was about 150,000 lux. It can be seen in this leaflet that each of the solarized areas (from 2½ to 13 hours) is surrounded by a distinct margin of starch, which was entirely lacking from the leaflet shown in figure 1. This starch

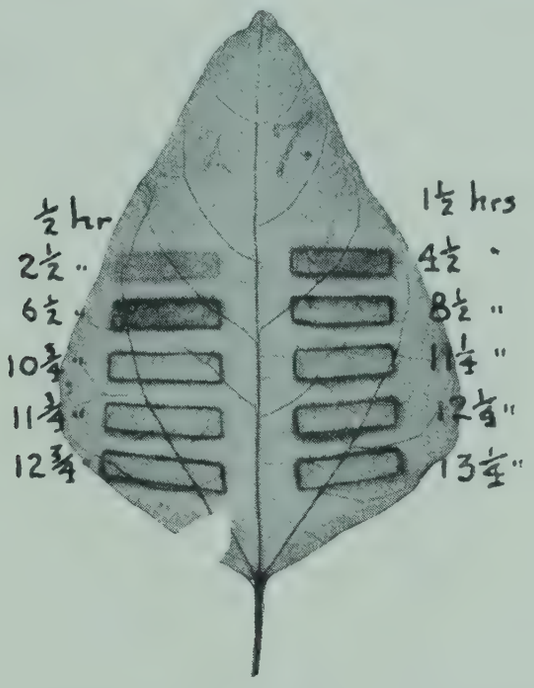


Fig. 2. Leaflet treated as was the leaflet in figure 1, except that the light intensity was greater. For further explanation see the text. Temperature 25–27° C. Light intensity about 150,000 lux.

margin is apparently similar to the darker line found by Ursprung in leaves exposed to direct sunlight and which he attributed to partial shading by the edge of the frame holding the leaf. When a piece of photographic paper was substituted for the leaf and exposed to the same illumination for a brief period, prints were secured (fig. 3) with

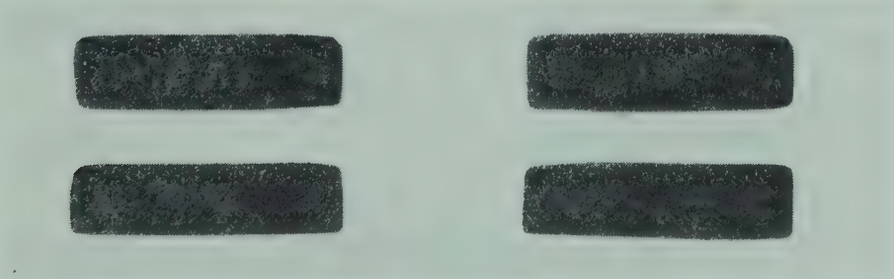


Fig. 3. Contact prints of four of the apertures through which the light fell upon the leaves. The contact prints are shown about twice their original size in the figure. Further explanation in the text.

boundaries so sharp as to indicate that the darker margins around the solarized areas of the leaves were not due to a penumbra, in the ordinary sense of the word.

Two explanations suggest themselves as to the cause of this starch margin. One is that sugar diffusing outward a little way from the illuminated area where starch formation is inhibited, is present in the dark part of the leaflet, just outside the lighted area, in concentration favorable to starch formation.

The other and more probable explanation is that, by reflection and refraction within the leaflet, light from the directly illuminated tissue spreads laterally beyond the boundaries of the aperture. This diffused light has, at certain distances from the edge of the directly illuminated area, intensities favorable to starch formation and yet too weak to cause solarization.

It is an interesting fact, observed in the treatment of the exposed leaves previous to staining with iodine, that as soon as the chorophyll has been removed and while the leaves are still in alcohol the starch becomes distinctly visible macroscopically. The starch margins of solarized areas, or the entire starch-filled areas, where solarization has not yet taken place, stand out by reason of their greater opacity and white color from the starch-free portion of the leaf. When the alcohol is replaced with water the starch-filled areas are no longer discernible unless the leaf is stained with iodine.

Returning to figure 2, we observe that the quantity of starch in the illuminated areas increases up to six and one-half hours. However, the light intensity in this experiment was clearly greater than the optimum for starch formation even for periods of six and one-half hours or less, for all areas show a distinct starch margin, even the 1½-hour area which shows no starch except in the margin.

The leaflet shown in figure 4 shows practically complete solarization of all the exposed areas. In areas 9, 11½, and 12½, dark lines of starch can be observed running across the solarized areas. These are due to a fine scratch on the glass of the cooling cell.

Now as to evidence bearing on the cause of solarization: Schroeder and Horn (1922, pp. 166 ff. and 1923, pp. 137 ff.) have attributed solarization primarily to water shortage in leaves exposed to light of high intensity. Sachs (1884, p. 14) himself observed *Helianthus* leaves on hot sunny days contained less starch in the afternoon than in the forenoon of the same day and interpreted this fact as due to wilting of the leaves. Neger (1915, p. 372), Schroeder and Horn, and others have shown that wilting hastens the disappearance of starch from starch-filled leaves. The most striking evidence of this has been furnished by Molisch (1921, pp. 340–344). Using various species, he

compared excised, starch-filled leaves kept in a very moist atmosphere, with similar leaves allowed to wilt, and found that the wilting leaves lost starch much more rapidly than those which retained their turgor.

Of scores of leaves used in the present experiments none have shown any evidence whatever of wilting. In view of the relatively small proportion of the total leaf area which was exposed to intense illumination, it might be contended that a very considerable water deficit might exist in the illuminated areas while the leaf as a whole

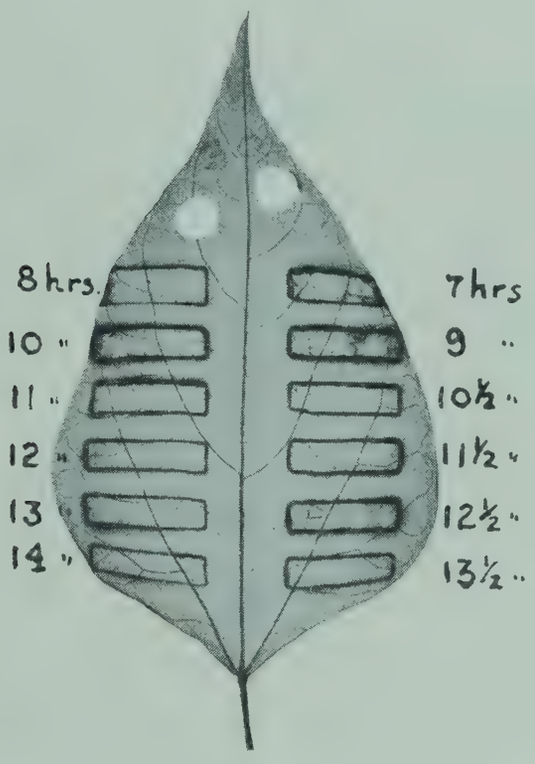


Fig. 4. Leaflet treated as were the leaflets in figures 1 and 2, except that the six shorter exposures were much longer than the corresponding exposures in the other two leaves. Temperature 23–25° C. Light intensity about 150,000 lux.

showed no evidence of loss of turgor. On that account the effect of shading very small areas of the leaf by means of fine wires, or single fibers from a black silk thread, laid across the illuminated areas has been tested. The wires used had diameters of 75 to 80μ and the silk fibers were 10μ in diameter.

Figure 5 shows, under considerable magnification, two of the illuminated areas of a leaflet shaded by such a wire and by a single silk fiber. The shadow of the wire can be clearly seen running across the solarized area. The shadow is black instead of white, as is the shadow of a wire across the starch-filled area of the leaf shown in figure 1. The shadow of the silk fiber, though only 10μ in diameter, may also be made out in several places on the illuminated areas of

this leaf. In the lower of the two areas shown, the image of the silk filament can be followed only part way across the solarized region, because for a portion of its course it coincides with a veinlet of considerable width. On account of the difficulty of handling a single silk fiber and fastening it in place across the surface of the leaf, tungsten wires, 19μ in diameter, were used instead of the silk fibers when this experiment was repeated. The greater opacity of the metal wires also favored their use.

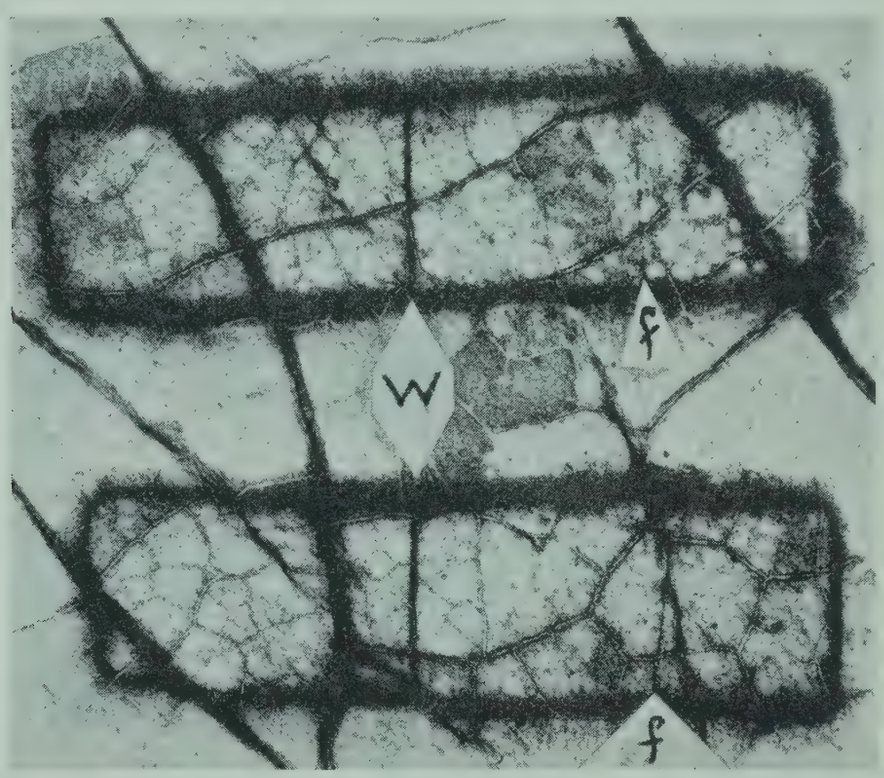


Fig. 5. Portion of a leaflet of scarlet runner bean showing two solarized areas traversed by the shadow of a wire (*w*) and of a black silk fiber (*f*). The angular, dark areas to the right of *w* and elsewhere in the unexposed and in the solarized regions owe their dark color entirely to air within the leaf. Exposure 8 hours. Temperature 26–27° C. Light intensity about 150,000 lux. × 11.

Figure 6 shows clearly that the shadow of a wire 19μ wide is sufficient to inhibit for many hours the process of solarization in the mesophyll tissue on which it falls.

The starch strip caused by the shadow was quite uniform in width, not varying much from the diameter of the wire itself, as shown by micrometer measurements which gave values of from 17 to 21μ.

Microscopic examination of free-hand sectons of living leaves of the scarlet runner bean shows that the diameter of the palisade parenchyma cells in a direction parallel to the leaf surface ranges from about 14 to 24μ. The spongy parenchyma cells are often from

30 to 35μ in diameter. It follows, then, that at many places along the starch strip, caused by the shadow, and at a given depth in the leaf, not more than a single cell falls under the shadow of the wire. At many other places, only parts of two cells are shaded. It seems very likely, then, that one part of a cell may be solarized while another part retains its starch. When wire of 10μ diameter or less is secured, an attempt will be made to show this more directly by means of microtome sections so stained as to show the starch grains within the chloroplasts.

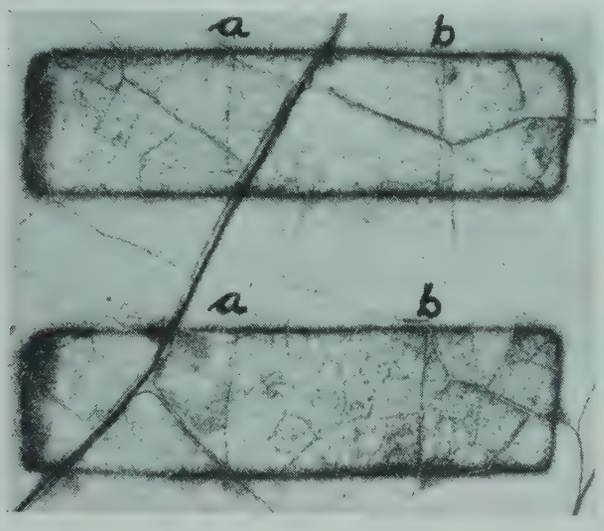


Fig. 6. Two of the solarized areas of a leaflet of *Phaseolus multiflorus* showing, at *a* and *b*, that the shadow of a 19μ wire is sufficient to prevent solarization. Temperature 29–30° C. Exposure 11 hours. × 4.

The retention of starch for many hours by so narrow a strip of cells bounded by solarized tissue, certainly shows that solarization is quite distinct from the disappearance of starch due to wilting. This also makes it highly unlikely that the disappearance of starch is due to high temperature in the illuminated areas of the leaves in our experiments, for no considerable temperature gradient can be maintained within the mesophyll of the leaf, between points 10μ (half of the diameter of the shadows) distant from each other. It would, then, appear that solarization is not the result of heating, or of water deficit induced by the illumination of the leaf tissue, but is due to a more direct effect of light upon the chloroplasts and perhaps also upon the rest of the illuminated protoplasm of the leaf cells.

Several ways suggest themselves by which intense light might reduce or inhibit the power of the chloroplasts to accumulate starch. One of the simplest would be by partial destruction of the chlorophyll. Photosynthesis might thus be so much retarded that the formation of

new starch would cease, while the conversion of the starch already present went on as usual or even more rapidly. Relative to the part which reduction in chlorophyll may play in solarization, I can thus far contribute only the observation that in my experiments solarization has never occurred without a distinct fading of the green color of the leaf. This was also observed frequently in leaves, such as that shown in figure 1, in which the exposures were too short or the light intensity too low to cause solarization.

This reduction in the depth of color of the leaf tissue is clearly apparent when, in the course of a solarization experiment, a fresh area of the leaf is exposed to intense light. Then, if the leaf is viewed from behind, so that it stands between the light source and the observer's eye, the contrast in color between the area just uncovered and the next lighted area, which has been exposed for an hour or more, is conspicuous. This partial bleaching does not involve the death of the cells, for attached solarized leaves may remain alive for weeks. Complete recovery of the original depth of color does not take place so far as I have been able to observe. Ursprung makes no mention of any bleaching in solarized leaves. His apparent failure to observe this was probably due to the absence of any very sharp boundary between the solarized and the non-solarized region in leaves illuminated by spectra. The fact that distinct, although not extreme, fading was apparent in all my experiments, even when the exposures were much less than would produce any sign of solarization, suggests strongly that destruction of chlorophyll may be at least partly responsible for the failure of the leaf to maintain starch in the solarized areas.

Saposchnikoff (1890, p. 240) and other investigators have shown that accumulation of the products of photosynthesis may inhibit further assimilation of carbon dioxide. Moreover, Tollenaar (1925, p. 46) in his experiments with *Tropaeolum* leaves floated on sugar solutions in the dark found that high concentration of glucose or sucrose (above 7 per cent of glucose or 15 per cent of sucrose) did not favor starch formation. Ursprung himself suggested that excessive accumulation of the products of photosynthesis may be responsible, at least in part, for the cessation of starch production in solarized leaves. High concentration of oxygen, liberated in photosynthesis, accumulation of sugar or even excessive quantities of starch in the green cells of the leaf may be responsible for the inactivation of the chloroplasts.

With the idea of throwing some light upon the relation of solarization to the accumulation of the products of photosynthesis, I have compared leaves supplied with less than the normal carbon dioxide concentration with others which were given more than the normal concentration.

The leaves compared were taken from the same or adjoining nodes or from corresponding nodes of two very similar plants and the carbon dioxide concentrations used were approximately 0.6 per cent

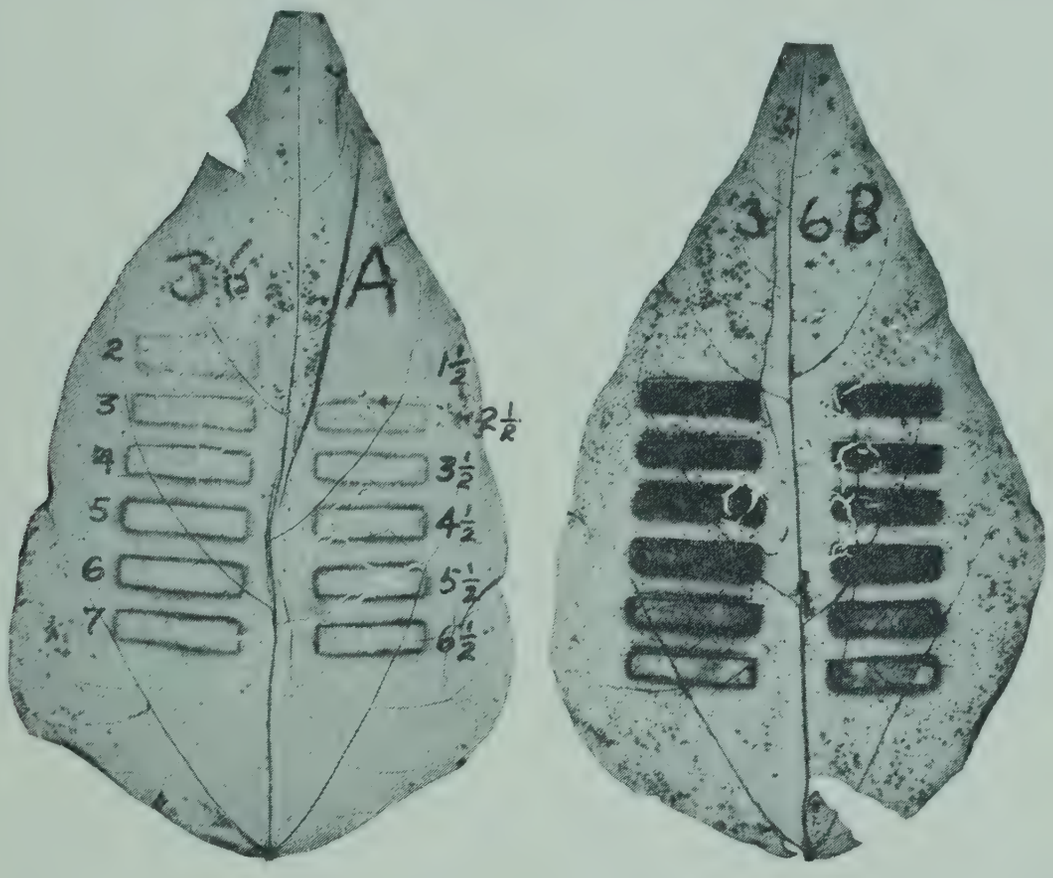


Fig. 7. Terminal leaflets of two leaves from the same node of a plant of scarlet runner bean. The leaflets were similarly treated except that, during the period of illumination which followed destarching, the leaflet to the left (36A) was supplied with air containing approximately .015 per cent CO_2, the one to the right with air containing approximately .6 per cent CO_2. The figures opposite the twelve exposed areas of leaf 36A indicate the periods of exposure in hours. Corresponding areas of leaf 36B were given the same exposures. Temperature 23–26° C. Light intensity about 150,000 lux.

and 0.015 per cent. The results were so striking and definite as to leave little doubt that increased carbon dioxide supply delays rather than hastens solarization.

Figure 7 shows two leaves of which the one to the right was given the greater quantity of carbon dioxide. When one-half the normal carbon dioxide concentration was supplied, all exposures, from one and one-half hours to seven hours, showed complete absence of starch

except around the margin. With the higher concentration starch was present in all the exposed areas up to seven hours and there was no evidence of solarization up to three or four hours.

If further repetitions of these experiments give the same results, it will be clear that solarization is not the result of the accumulation of any of the products of photosynthesis but that, on the contrary, it is due to a direct reduction of the efficiency of the chloroplasts in starch formation. This reduced efficiency, far from being accentuated by the increase of the products of photosynthesis, owing to enriched carbon dioxide supply, is largely offset by added carbon dioxide.

I have made repeated attempts to secure solarization in leaves which were starch-filled at the beginning of the experiments. These have given only negative results. I think that my evidence on this point is sufficient to justify the conclusion that solarization takes place more slowly, if at all, when the leaves are starch-filled to begin with. Even if intense illumination largely inhibits the formation of more starch in such leaves, disappearance of the starch in the lighted areas may be prevented by the relatively high concentration of soluble carbohydrates in the whole leaf. This would presumably delay the removal of the products of starch solution from the lighted areas and thus retard the disappearance of starch from these areas.

The absence of solarization in my experiments with starch-filled leaves gives further support to the conclusion that solarization is not the result of excessive accumulation of starch or soluble carbohydrate products of photosynthesis.

Repetition of many of the experiments reported here is needed to check the results already secured. We may, however, state the following tentative conclusions relative to solarization in the leaves of *Phaseolus multiflorus*. This phenomenon is due to a reduced power of carbon assimilation, or at least of starch formation, by the chloroplasts. This reduction is due not to the accumulation of the products of photosynthesis nor to water deficit, nor to high temperature, but to a direct effect of absorption of light energy by the chloroplasts. It may be in large part the result of reduction in the amount of chlorophyll which always accompanies light exposure sufficient to cause solarization.

It is apparent that in addition to further checking of the results already secured, several questions not yet touched upon should be studied before the problem can be considered as in any sense completed. Experiments on the effect of increased oxygen concentration

on solarization should be made, although the results of increase in carbon dioxide concentration seem to indicate that the oxygen liberated in photosynthesis is not responsible for solarization.

LITERATURE CITED

Boysen-Jensen, P., and Müller, D.
1929. Die maximale Ausbeute und der tägliche Verlauf der Kohlensaüre-assimilation. Jahrb. f. wiss. Bot., **70**:493–502.

Horn, T.
1923. Das gegenseitige Mengenverhältnis der Kohlenhydrate im Laubblatt in seiner Abhängigkeit vom Wassergehalt. Bot. Ark., **3**:137–173.

Molisch, Hans.
1921. Ueber den Einfluss der Transpiration auf das Verschwinden der Stärke in den Blättern. Ber. d. d. bot. Gesell., **39**:339–344.

Neger, F. W.
1915. Die Stärkeökonomie der grünen Pflanzen. Naturwiss. Wochenschr. für Forst- und Landwirtsch., **13**:370–380.

Pringsheim, N.
1879–1881. Ueber Lichtwirkung und Chlorophyllfunktion in der Pflanze. Jahrb. f. wiss. Bot., **12**:288–437.

Sachs, Julius.
1884. Ein Beitrag zur Kenntniss der Ernährungsthätigkeit der Blätter. Arb. d. bot. Inst. in Würzburg, **3**:1–33.

Saposchnikoff, W.
1890. Bildung und Wanderung der Kohlenhydrate in den Laubblättern. Ber. d. d. bot. Gesell., **8**:233–242.

Schroeder, H., and Horn, T.
1922. Das gegenseitige Mengenverhältnis der Kohlenhydrate in dem Laubblatt in seiner Abhängigkeit vom Wassergehalt (Vorläufige Mitteilung.). Biochem. Ztschr., **130**:165–198.

Tollenaar, D.
1925. Omzettingen van koolhydraten in het blad van Nicotiana Tabacum. Dissertation, Wageningen.

Ursprung, A.
1917. Ueber der Stärkebildung im Spektrum. Ber. d. d. bot., Gesell., **35**:44–82.

CHROMOMERES OF LILIACEOUS PLANTS

BY

JOHN BELLING

University of California Publications in Botany
Volume 16, No. 5, pp. 153–170, 11 figures in text
Issued January 20, 1931

University of California Press
Berkeley, California

Cambridge University Press
London, England

CHROMOMERES OF LILIACEOUS PLANTS*

BY

JOHN BELLING

INTRODUCTION

It is not easy to make preparations that demonstrate the ultimate chromomeres, because the chromomeres of neither animals nor plants show well in sections. For the study of chains of chromomeres, smears seem to be necessary. But not every plant preparation treated by the best methods shows the chromomeres equally well. Some plants give good results when in a state of rapid development. (This may be insured, for Lilium and others, by raising the temperature of the room.) Iron-acetocarmine preparations will show ultimate chromomeres only if efforts are made to obtain superior fixation. Rather few pollen-mother-cells may be pressed into a drop of iron-acetocarmine, and left for some time to fix. When the cover is put on, the amount of liquid is to be adjusted so that there is a slight pressure on the pollen-mother-cells. Then, after some days, some of the cells at late pachytene may show rows of chromomeres clearly, especially those cells whose walls were more or less split in mounting (fig. 1). Smears, carefully fixed with chrom-acetic-formalin and stained with iron-brazilin, will often fail to yield good pictures of chromomeres, in all but a few cells. Some of the cells are always better fixed than the others (fig. 2). This is especially the case with large pollen-mother-cells like those of Lilium, and less so with smaller cells like those of Rhoeo.

In the writer's first fixations of smears of Lilium, only plain coiled strings appeared at the pachytene stage, and there was difficulty in getting the pollen-mother-cells to stick to the slide. After overcoming this trouble, the writer found some few cells with strings of apparently single chromomeres at pachytene. By striving for better fixing, he finally obtained a number of cells, out of those on the slide, in which the synapsed chromomeres of each homologous chromosome were distinctly separate, and could be counted; while the fine connecting

* This paper presents the results of cytological work done under the auspices of the Carnegie Institution of Washington.

threads were also visible. Lilium, however, is a difficult plant to fix well. But the pachytene of *Fritillaria* species growing wild in California is comparatively easy to fix in smears, so as to show the double chromomeres separated and countable. For Agapanthus and Aloë, less expenditure of time is required to get good results than for Lilium. The writer has also made satisfactory preparations of the ultimate chromomeres of Allium, Hyacinthus, Scilla, Rhoeo, Tulipa, Kniphofia, Tradescantia, Narcissus, and other liliaceous plants.

For the stages of meiosis the following terms are used, mostly after Wilson: *leptotene,* with the double number of threads, and the chromomeres undivided; *zygotene,* with the threads partly synapsed, and partly in loops; *early pachytene,* with all the chromomeres synapsed, but with no trace of the secondary split; *late pachytene,* with the secondary split showing in the homologous chromomeres; *diplotene,* with the synapsed chromomeres separating, together with their connecting threads, to form loops—the separation occurring, in the writer's opinion, at the primary split only; *early diaphase,* shortened bivalents, with zigzagging of the chromonemas; *middle diaphase,* shorter bivalents, with much zigzagging; *late diaphase,* bivalents shorter and thicker, but still scattered; *metaphase,* bivalents arranged in the equatorial plane. A *chromomere,* or *ultimate chromomere,* is one of the leptotene beads, or the corresponding body at early pachytene. At late pachytene, each chromomere is splitting into two *chromioles,* at the *secondary split.*

GENES AND CHROMATIN

For the last three years the writer has been working on the early stages of meiosis in as many liliaceous plants as were favorable. Since the method was practiced of staining the chromomeres with iron-brazilin, it was possible to count them in Lilium, Aloë, and Agapanthus. It was thus ascertained that there were up to about 2500 pairs of chromomeres (and doubtless genes also) in the pollen-mother-cells (and hence in all other diploid cells) of Lilium. Subsequent work has only confirmed this. At leptotene, minute, closely set beads (chromomeres) of different sizes have been demonstrated by the writer in Lilium, Allium, Hyacinthus, and several other plants. At zygotene, the homologous chromomeres become paired (synapsed). At early pachytene, a successful case of destaining disclosed a minute, about submicroscopic, black dot at the center of each chromomere.

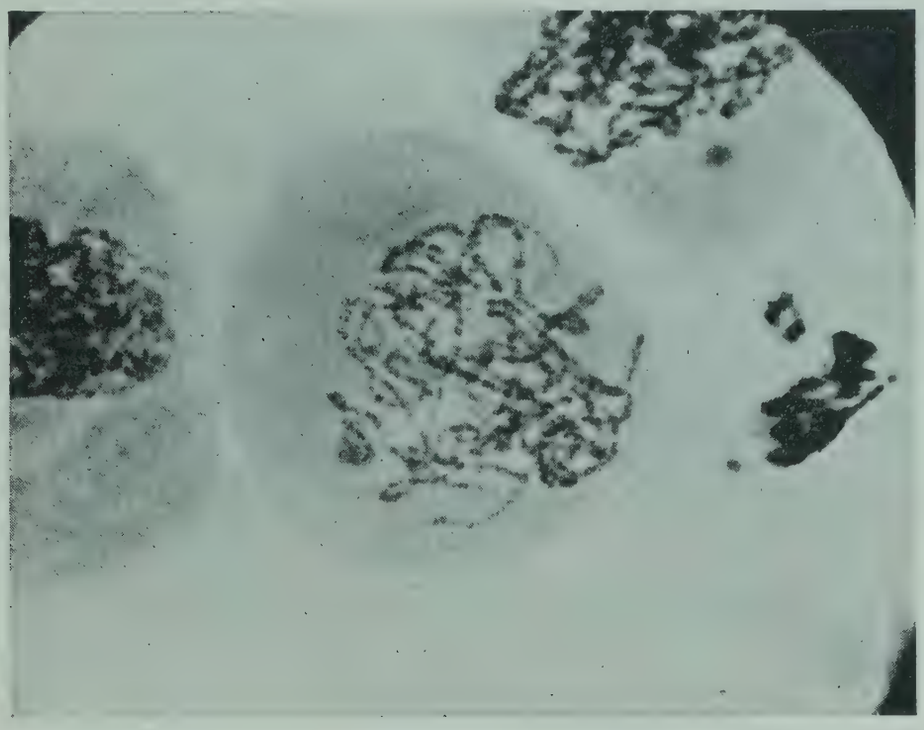


Fig. 1. Photograph of late pachytene of *Aloë striata*. Fixed and stained with iron-acetocarmine. Squeezed flat, and photographed with Zeiss' Phoku camera, and water-immersion objective 70, with subsequent enlargement. This preparation shows the beaded structure, but not the details of the chromioles. Several previous workers have obtained figures like this, in both plants and animals, with various fixatives.

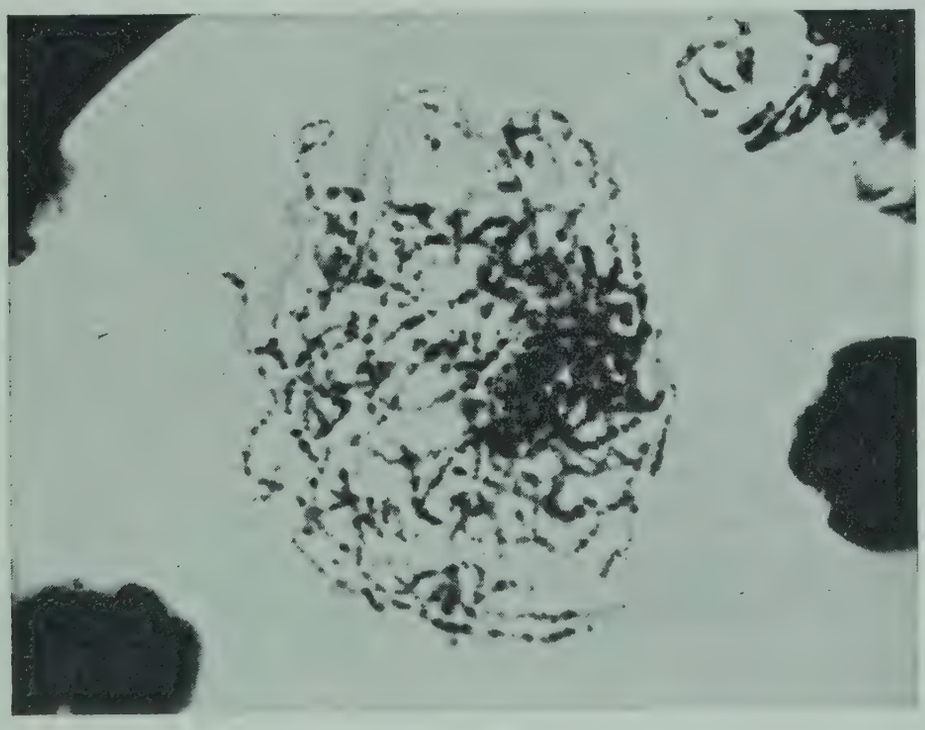


Fig. 2. Photograph of late pachytene of *Lilium pardalinum*. Fixed with chrom-acetic-formalin, stained with iron-brazilin, and mounted in immersion oil. Photographed with the 90 apochromatic objective of 1.3 aperture. This cell shows the chromomeres double in many places, but this is not reproduced in the photograph.

This is either a bare gene, or close to one. Hence a chromomere is a gene with a covering of chromatin, usually different in volume for different genes. In late pachytene, each chromomere begins to divide into two, the amount of chromatin having further increased (fig. 3). (The chromatin which thus forms a separate envelope around each gene, at the late pachytene will be called here *gene chromatin.*) After the primary split has opened out at diplotene, and especially after the threads begin to zigzag at diaphase, *extra chromatin* binds the zigzags together, at first partly and in clumps. (These clumps have been called "compound chromomeres.") At late diaphase and at early

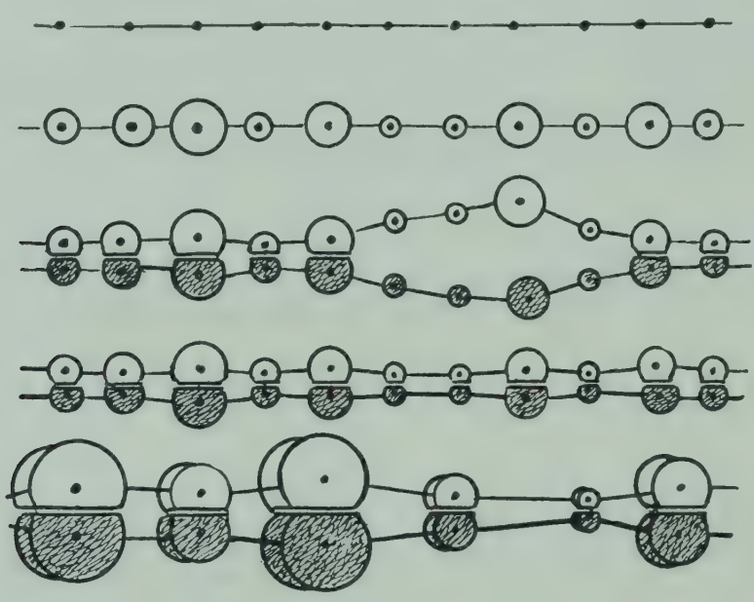


Fig. 3. Diagram of chromonema (gene-string) of Lilium, from pre-leptotene till late pachytene. *First line:* thread during pre-leptotene. The thread often appears structureless, not staining deeply with iron-brazilin. However, dots may sometimes be seen in it, representing the genes. *Second line:* diagram of leptotene thread of Lilium. The connecting portions between the chromomeres are usually unstained, and the chromomeres somewhat closer together than in the figure. The position of the gene is marked in each chromomere by a dot. *Third line:* zygotene, showing homologous chromomeres synapsing, before and after a loop. *Fourth line:* early pachytene, with no trace of the secondary split, and all chromomeres synapsed. *Fifth line:* late pachytene, with the secondary split showing. The new connecting fibers are not yet visible.

metaphase this extra chromatin reaches its maximum. At early anaphase, the extra chromatin partly dissolves and disappears, leaving the chromosomes and chromatids more free to separate. During the telophase and interphase, much of the extra chromatin goes; but the gene chromatin remains. The chromatin is distributed uniformly into the four cells which result from the second division of meiosis.

So far as the writer has seen in the somatic divisions of Galtonia, Rhoeo, and Tradescantia (cf. also Belar, 1929), it seems probable that

the division of the chromomeres into chromioles, and their equal distribution to the daughter cells, are much the same as in the secondary split of meiosis.

Hence, besides the regular segregation of genes paralleling the segregation of Mendelian factors, we have the regular segregation of gene chromatin, paralleling both. If the chromatin which collects around each gene is as different in quality as it is different in quantity, or if it contains different substances in different chromomeres; then materials scattered in the nucleus, or perhaps through the cytoplasm, can segregate out and be distributed along with the genes. Thus the gene, which segregates apparently free from nuclear or cytoplasmic influence, is accompanied by an envelope of chromatin, many times larger in mass, which need not be free from the influence of the nucleus or cytoplasm from which it was collected.

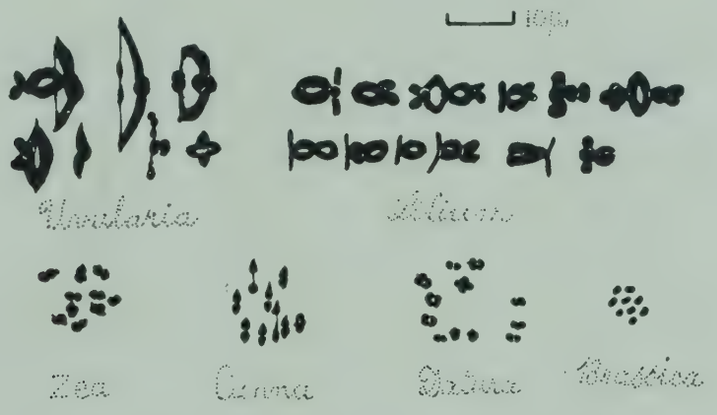


Fig. 4. Camera drawings of the first meiotic metaphase, in four monocotyledons and two dicotyledons, at approximately the same magnification. It is evident that two of the monocotyledons have many times the total volume of chromatin of the other two, and also of the two dicotyledons.

The students of variegation may, therefore, perhaps use this "gene chromatin" in their hypotheses in certain cases (not due to fractions of a chromosome), instead of "genomeres," of which the writer has found no microscopical evidence. Also those who are looking for some hypothesis to fit the changes of cells in cellular ontogeny may find it advantageous to consider the chromatin, as the only substance except the genes which regularly segregates equally at cell division and at meiosis; a statement which cannot be made of chondriosomes, or Golgi bodies, or even of all cases of centrosomes.

In Lilium the extra chromatin has been calculated to be, at metaphase, about ten times the quantity of the gene chromatin at pachytene (Belling, 1928*c*). In some plants, such as Fritillaria, the

gene chromatin is in relatively larger amount than in Lilium. In other plants, such as *Scilla peruviana,* there is so little gene chromatin that the chromomeres at pachytene are near the limit of visibility.

In some flowering plants (even among monocotyledons) the total amount of chromatin at metaphase in one plant may be even more than fifty times that in another species (polyploids being excluded). We may compare, for instance, Lilium and Canna, or Uvularia and Zea (fig. 4). The total amount of chromatin often bears a relation to the size of the somatic cells. These cells are unusually large in Lilium. The writer measured the volume of chromatin and of cytoplasm at the first metaphase of meiosis in eleven plants of different species. There were wide exceptions to a constant ratio of the volume of chromatin to the volume of the pollen-mother-cell. Thus Canna and Datura, with nearly equal amounts of chromatin, have very unequal volumes of cytoplasm in the pollen-mother-cells. M. Navashin has shown, however, for thirteen species of *Crepis,* that the total amount of chromatin in cells of the cortex of rootlets is proportional to the volume of the cytoplasm of these cells (Babcock and Navashin, 1930). Hence, since there is apparently some close relation between mitotic and meiotic chromatin, we may perhaps regard the amount of chromatin at meiosis as related to the amount of cytoplasm in somatic cells.

It is obvious that the total volume of chromatin at first metaphase bears no relation to the number of genes. Suppose Lilium to have fifty times the total amount of chromatin that Canna has, it cannot, however, be inferred that, because Lilium has about 2500 different genes, Canna has only 50. Nor does the volume of *gene chromatin* bear a relation in different plants to the number of genes; as may be seen by comparing *Scilla peruviana* with *Fritillaria lanceolata,* where the numbers of ultimate chromomeres seem on inspection to be much the same, while the amounts of gene chromatin are markedly different. In different chromosomes of the *same plant,* however, the length of the chromonema, which would be more or less proportional here to number of genes, would probably determine the volume of both gene chromatin and extra chromatin. So the relative numbers of genes in any chromosome or part of a chromosome of the same plant, may be usually roughly proportional to the length or volume of such chromosome. Also in haploids, autotriploids, autotetraploids, etc., we know that the total number of genes is increased or diminished correspondingly with the total volume of chromatin; and also, as has been shown in Datura (Belling and Blakeslee, 1923), etc., correspondingly with the volume

of cytoplasm. However, these are relations within the species, and do not necessarily apply to *different* species (which are not polyploids). Hence it is possible that different liliaceous plants (excluding polyploids) may have about the same number of genes; for there is apparently no known reason why they should differ *greatly* in this respect, though the numbers and sizes of their chromosomes and the total amounts of chromatin may be very different. From the examination of the ultimate chromomeres of about a dozen genera of liliaceous plants, the writer has the impression that they do not differ much in number, though the numbers of chromosome pairs varied from 6 to 15, and the amounts of chromatin were quite different.

Even in a polyploid plant, however, the genes may perhaps not remain indefinitely at the original high number. Taking an autotetraploid, for example (and the same would apply in some degree to an amphidiploid), there are four genes for each character difference. Two of these are doubtless superfluous, and are more or less shielded by the other two from lethal selection. So recessive mutations (lethal in the absence of the normal gene), as Muller (1928) has shown, may tend to take the place of the shielded genes. Since many such mutations are probably, in the writer's opinion, losses of a vital gene, the two extra genes may tend in time to be lost. This, perhaps, is why there are not so many triple or quadruple genes as might be expected, even in such comparatively recent tetraploid or hexaploid forms as *B. bursa-pastoris* and *Triticum vulgare*. In such cases the gradual loss of genes might perhaps bring about a gradual shortening of the chromosomes, such as Delaunay (1926) postulated when tracing the origin of certain genera of plants.

A MODIFIED WORKING HYPOTHESIS FOR CROSSING-OVER

The writer's previous working hypothesis for crossing-over (Belling, 1928*a*) was framed after he had studied the diplotene and diaphase, but before he had succeeded in staining the chromomeres at leptotene, zygotene, and pachytene. Hence more stress was naturally laid on the threads than on the chromomeres. Work during the last three years has shown that the chromomeres are the important parts of the threads, the fine connecting fibers being apparently a product of the chromomeres. For such fibers may be seen often to have grown transversely between homologous chromomeres, where they must have been formed *de novo*. So it is likely that they will grow afresh longi-

tudinally between chromomeres adjacent in the rows, where connecting fibers may be absent. When the chromomeres are divided by the secondary split into two chromioles, in each case one of these chromioles can remain connected by the old longitudinal fiber; but the sister chromiole requires a new longitudinal fiber (fig. 3). This may arise, presumably, either by the longitudinal division of the previous fiber, or by the formation of a new fiber (fig. 5). That new longitudinal fibers may sometimes be formed is known, because in every case of crossing-over (and crossing-over is a *vera causa*), new longitudinal fibers *must* arise at the point of crossing-over, and could not arise by the splitting of old fibers. There are other cases, too, in which longitudinal fibers arise *de novo*. When this possibility is kept in mind, a modified hypothesis for crossing-over comes into view.

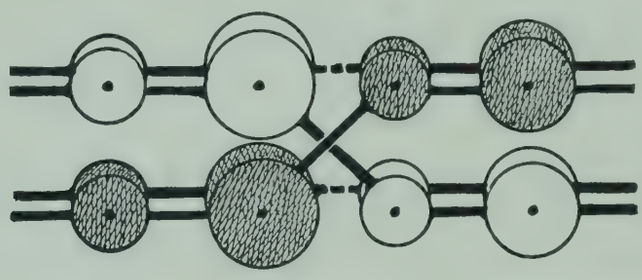


Fig. 5. Diagram illustrating the writer's modified hypothesis of crossing-over. At late pachytene, the two homologous chromosomes, or strings of chromomeres (one white, the other shaded), show a half-twist. After the secondary division of the chromomeres, the new chromomeres become connected by new fibers. These new fibers at the half-twist take the shortest way (broken lines). This constitutes crossing-over.

At the pachytene stage in Lilium, the writer not seldom remarked an X formed by a half-twist which had occurred probably at the zygotene stage. Similar half-twists, between two synapsed chromomere pairs have been previously figured (Gelei, 1921). When the chromomeres synapse individually, it is too much to expect that the two rows will lie always in one plane. There are as yet no proofs of any special lateral *orientation* of the genes in a string. That there is no end-to-end orientation of the genes follows from the facts that a segment of a chromosome can be inverted (Sturtevant, 1926); also that two chromosomes can be combined by homologous ends (L. V. Morgan, 1922); and that parts of non-homologous chromosomes can be joined to form a new chromosome (Sturtevant and Dobzhansky, 1930; Belling, 1927). Hence half-twists, in the presumed absence of any lateral orientation of the genes, may be regarded as occurring regularly in most pachytene coils. (The average distance between half-

twists may depend mainly on physical causes, including the mutual attraction of homologous genes, or chromomeres.) At each such half-twist, which may be in one direction as often as in the other, the two threads form an X (figs. 5 and 9). This is before the secondary division has occurred, and while the constituent chromomeres of the pairs and their longitudinal connecting threads are single. Figure 5 shows that at late pachytene, when the chromomeres have split but before the chromioles have separated, the new longitudinal threads will probably take the shortest way and be attracted to the chromomeres closest to them in a straight line. This is all that is needed as a cause of crossing-over, and it postulates little beyond what has already been seen.

In figure 5 the new connecting threads are not distinguished from the old, except at the twist. However, it is probable that their position is determined by chance. This will make no difference in the longitudinal threads; but, when there is a half-twist, it will probably be a matter of chance (for each separate chromiole out of the four pairs of chromioles concerned) whether there is a longitudinal or oblique attachment. Then it would follow that any of the four chromatids concerned has an equal chance (at the half-twist) of crossing over or of not crossing over.

Any working hypothesis to account for chiasmas, that does not include crossing-over may, in the writer's opinion, be safely rejected; for crossing-over (which is a known fact) must, on any probable hypothesis, be itself a cause of chiasma formation. On the present hypothesis, the two cross-over chromatids are the ones that pass straight on; and the chromatids which form the X are non-cross-overs.

LEPTOTENE CHROMOMERES

The leptotene was especially studied by the writer in Lilium, Allium, and Hyacinthus. Late leptotene chromomeres in Lilium were equal to, or smaller than, those in zygotene or in earliest pachytene (fig. 6), and markedly smaller than those of late pachytene. The writer considers that the moniliform coils figured as leptotene in Lilium by some writers are probably pachytene. For the chromomeres at leptotene in Lilium are difficult to fix well; and are as close together as, or closer than, the chromomeres at earliest pachytene (fig. 6, left), which measured 0.44 micron from center to center. This is only two-thirds of the distance between chromomere centers at late pachytene

in Lilium (Belling, 1928*c*). The leptotene chromomeres show no split lengthwise, nor any trace of such split. Hence the union at zygotene is between homologous chromomeres, and not between homologous chromioles, as one author has lately suggested.



Fig. 6. Camera drawing of early and late pachytene of *Lilium pardalinum*. On the left, portions of early pachytene threads; on the right, a piece of a late pachytene coil, more widely spaced than the average. Note differences in size.

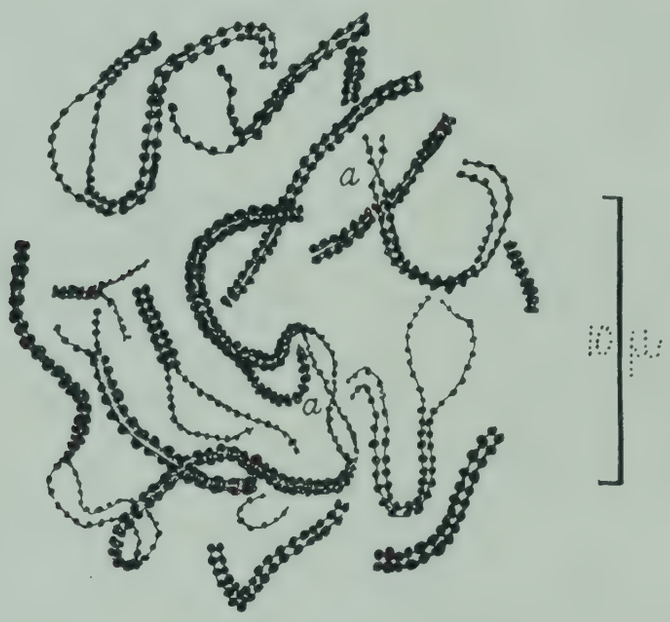


Fig. 7. Camera drawing of the zygotene of *Allium triquetrum*. Only the upper coils of the cell were drawn. In two places (marked *a*) the leptotene threads form a half-twist. Smear preparation, fixed with chrom-acetic-formalin, stained with iron-brazilin, and viewed with the 100 fluorite objective of Zeiss.

ZYGOTENE CHROMOMERES

At zygotene, chromomeres of corresponding sizes, and only these, have been seen to synapse, in Lilium, Allium, and Hyacinthus. Sometimes the synapsing threads leave, for a time, one, two, or more open loops in any one bivalent (fig. 7). The presence of these loops seems

to show that there is a special attraction between homologous chromomeres; for otherwise we should expect to see *non-homologous* chromomeres synapsed in a row, on one side or other of some of the loops. Thus the different sizes of the chromomeres may be taken as a sign of different qualities. Sometimes it appeared as if zygotene synapsis started mainly on one side of the cell. This would be expected if it started at the ends of the chromosomes, as in Dendrocoelum (Gelei, 1921); for, since the last mitotic division, the attachment points naturally tend to be near one pole of the cell, and the ends of V-shaped chromosomes near the other pole (cf. Belar, 1929). At the end of zygotene, the chromomeres have all synapsed.

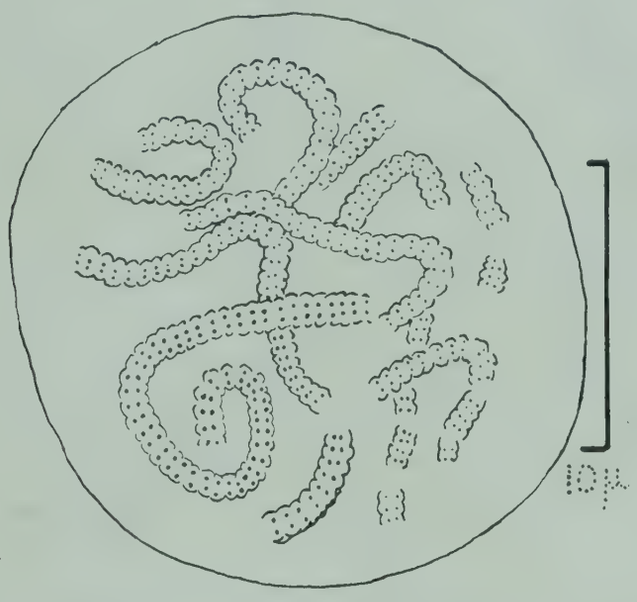


Fig. 8. Early pachytene of *Allium triquetrum,* fixed and stained as in figure 7; then mounted in hyrax, which slowly destained it. Cell squeezed quite flat by pressure on the cover. The chromomere cores (or genes) were visible as minute (probably submicroscopic) dots, one in each chromomere. Camera drawing, with the 100 fluorite objective.

CHROMOMERES OF EARLY PACHYTENE

At early pachytene (fig. 6, on the left), the sizes of the chromomeres in Lilium were about the same as in zygotene, but they gradually increased until late pachytene when the thread was about one and a half times its previous length, the difference between large and small chromomeres becoming more marked. The writer has found no sign of the secondary split in early pachytene. On slowly destaining the early pachytene of *Allium triquetrum,* mounted in hyrax and pressed flat, there were seen in the thread two, and only two, rows of minute black dots, one dot in the center of each chromomere (fig. 8). Several

cells showed this stage in the preparation, and in all there were the same two rows. These dots (or cores of chromomeres) were bodies as close to being genes as could well be and still be visible. This demonstrates that the genes and chromomeres had not yet entered on the secondary split. It agrees with Gelei's results (1921).

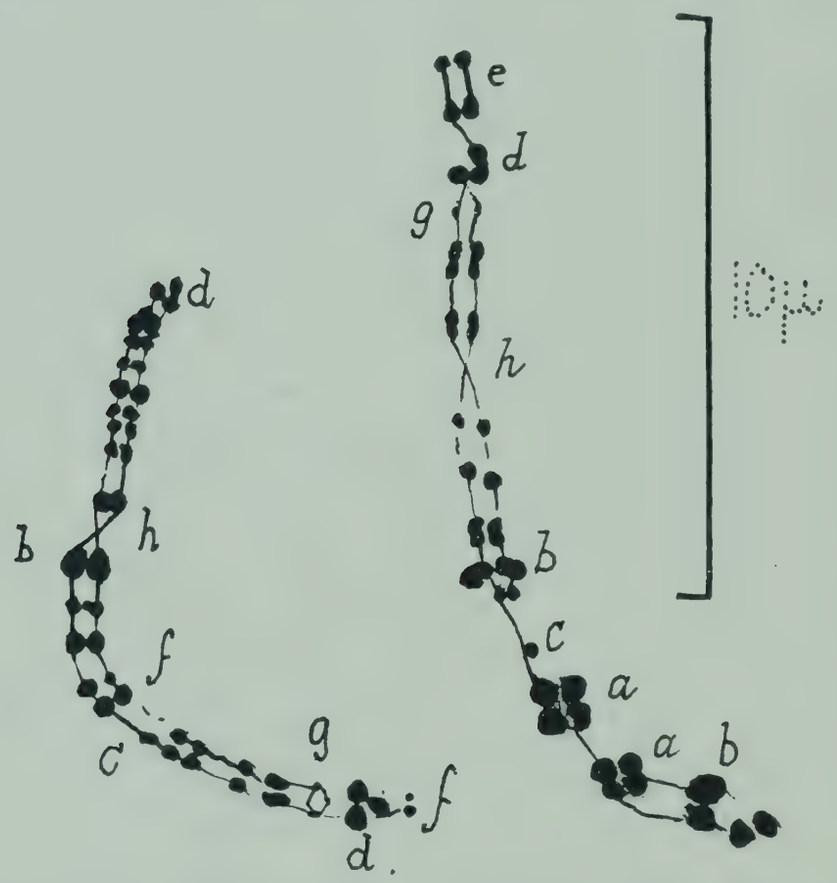


Fig. 9. Camera drawing of late pachytene of *Lilium pardalinum,* from a cell in which the chromomeres were well separated. Drawn with the 90 apochromatic objective of 1.3 aperture. This slide has also been examined with the monobromide of naphthalin objective of 1.6 aperture. Iron-brazilin stain was used, and the smear was mounted in immersion oil.

CHROMOMERES OF LATE PACHYTENE

At late pachytene in Lilium (fig. 9), the differences in size of the chromomeres in the row, which were demonstrated by the preparations of leptotene, zygotene, and early pachytene, are much increased. These differences are also especially clear at late pachytene in Fritillaria; and may be observed, though not so strongly marked, in the other liliaceous plants examined by the writer. The exaggeration of these differences, in Fritillaria and Lilium is doubtless due to the greater growth in length of the chromonema in these two genera, and the larger amount of chromatin. Many liliaceous plants have their

chromomeres so close together in late pachytene that it is difficult to elucidate the structure of the beaded threads. However, in Lilium, rare cells are found in which, in some of the coils, the chromomeres are sufficiently spaced apart for profitable study. From such a cell figure 9 was drawn. Only two longitudinal fibers were perceptible here, and but barely perceptible; the representation by black lines in the drawing being too conspicuous. The chromomeres, on the other hand, were deeply stained. The largest chromiole was nearly half a micron across, and the smallest seemed about one-eighth of this. There are visible double dumb-bells (fig. 9*a*), showing that the secondary split is not finished, while the primary split remains open as usual; also similar forms seen obliquely, or almost end on (fig. 9*b*); also cases where, in the writer's opinion, only one chromomere is present, without a homologous partner, which is to be inferred from the chromomere in question being on one side only of the connecting fibers (fig. 9*c*); also chromomeres (fig. 9*d*), apparently two in number on one side, linked by cross bars to one on the other side (which may possibly be a case of two dumb-bell-shaped chromomeres separated at one end); also cases where one pair of chromomeres is connected by strong longitudinal bars with another non-homologous pair, usually of different size (fig. 9*e*); also cases (fig. 9*f*) where one partner is smaller than its fellow (in the writer's opinion, this is not due to differences of staining, but is a true size difference); and, finally, cases where there are two minute homologous chromomeres, usually connected by two transverse threads about as wide as the chromomeres (fig. 9*g*). There are also places in the late pachytene of Lilium where the connecting threads form an X, indicating the presence of a half-twist (fig. 9*h*). Several of these eight occasional phenomena have been seen in other plants, especially Fritillaria and Aloë.

CHROMOMERES AT DIPLOTENE

The diplotene stage has been especially studied in Lilium, Aloë, Allium, Hyacinthus, Fritillaria, and Agapanthus. The threads separate into loops at many places, leaving many temporary points of junction (fig. 10). The points of junction diminish in number as the threads separate more, until only comparatively few are left, most of which are probably chiasmas (Belling, 1928*a*). In figure 11 we have a special case in which the extra chromatin has not yet involved the chromomeres and so rendered them indistinguishable, as is often the

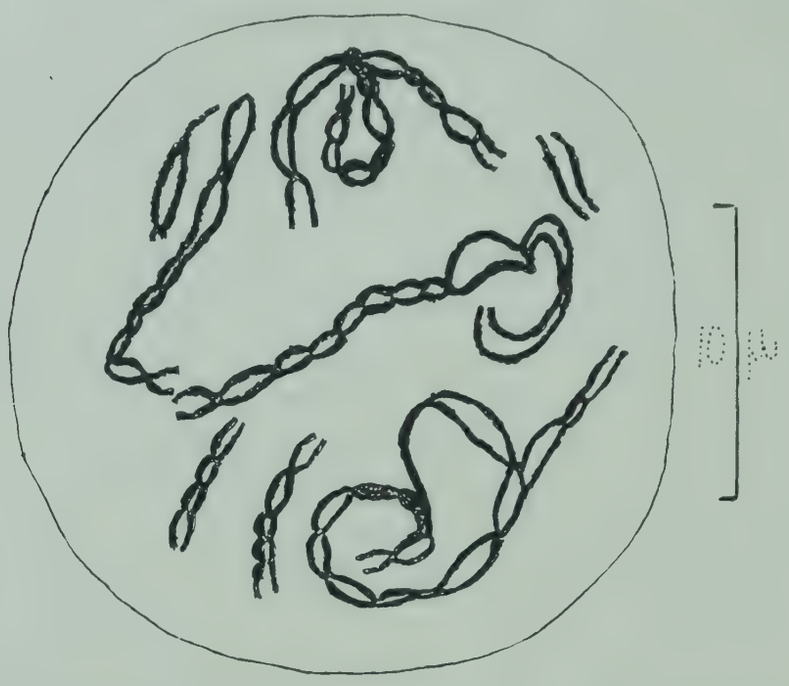


Fig. 10. Early diplotene of *Allium triquetrum*. The chromomeres are close together and connected with extra chromatin, so that they are not easy to distinguish. There are many nodes, mostly temporary, between the two homologous chromosomes. Fixing, etc., as in figure 7.

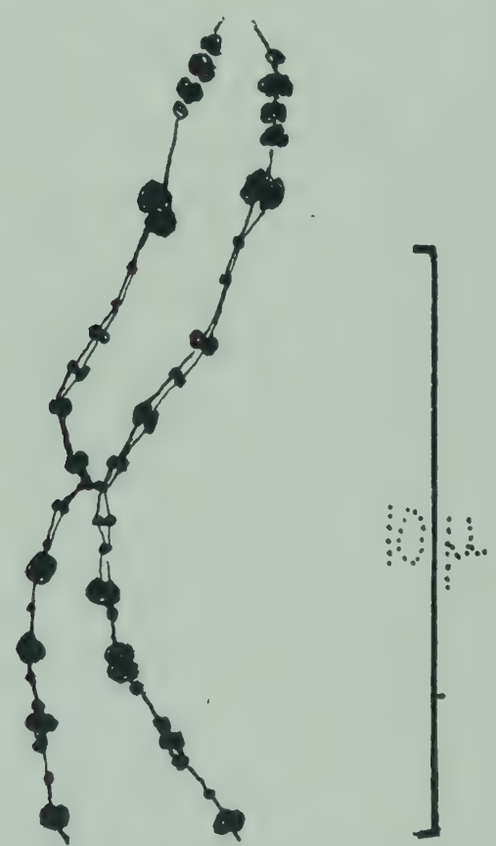


Fig. 11. Camera drawing of a selected portion of the diplotene coils of *Fritillaria lanceolata*. Twenty-three chromomeres on one side match in size their homologues on the other side, from which they have just been separated. The secondary split is visible in many fibers and chromomeres on each side. Two small chromomeres occur at the chiasma. Fixation, etc., as in figure 9.

case in late diplotene. Here twenty-three chromomeres on one side are equal in respective sizes to their twenty-three late partners on the other side. Many of the chromomeres figured show the secondary split, all having already divided into two chromioles. In many places, too, the new longitudinal connecting threads are visible. This specimen is from *Fritillaria lanceolata.*

CHROMOMERES AT DIAPHASE

At early, middle, and late diaphase, the chromonemas take a zigzag form, which has been demonstrated in Lilium and some of the other liliaceous plants, and is clear in Rhoeo (which shows only one chromonema at this stage). However, destaining in hyrax of the late diaphase of Aloë showed finally some of the ultimate chromomeres in each homologous chromosome bounding the loops; and further destaining led to the visibility of minute dots, which were nearly genes, and which were in twos in each homologue. These dots were doubtless the result of the secondary split in each homologue.

DISCUSSION OF RESULTS

Enzio Reuter (1930), in his excellent historical summary regarding chromomeres of all kinds, refers to no less than sixty-seven zoological or botanical writers who recognized one to many granules in some stage of the chromosomes. In many of these cases, as in the hemipteron studied by Reuter himself, the chromomeres in question were not the ultimate chromomeres but consisted of one or more lumps in the mature, or nearly mature, chromosome. They were doubtless compound chromomeres, like those seen by some methods of preparation in the metaphase of Tradescantia, or the anaphase of Hosta (Belling, 1925). Ultimate chromomeres have been more or less clearly seen by several investigators, and probably most clearly by Gelei (1921) and Wenrich (1916, 1917) in animals, by Newton (1927) and the writer (1928*b*, *c*) in plants.

Gelei, in *Dendrocoelum lacteum,* using smear preparations of ova, found, with a special stain, that chromomeres appeared in the early leptotene threads. There were many small and some large chromomeres. By measuring the fourteen leptotene threads, he found that they were of seven different sizes, two of each size. They were over four times as long as the corresponding chromosomes at the preceding

oögonial metaphase. Synapsis (conjugation) began at the ends of the chromosomes. The chromomeres when first coming into contact put forth mutual projections, which united to form a cross-thread. The ribbon resulting from the synapsed chromomeres showed the two synapsed rows of chromomeres on the broad side; while looked at edgewise, where it was of half the breadth, it showed only one line of chromomeres. But, later, the chromomeres extended down from the plane of the ribbon, and then the filament became of square section; showing in one plane two rows of chromomeres separated by the primary split, and in the plane at right angles cross-bars not yet, or barely, showing the secondary split. Large and small chromomeres were clearly seen at this stage also; the large having synapsed with large, and the small with small. X's were visible in early pachytene, formed by half-twists between synapsed pairs of chromomeres.

Wenrich (1916) demonstrated that in a bivalent of Phrynotettix, at late pachytene, there was the same serial arrangement of large chromomeres in different cells, and hence probably of small chromomeres also.

On Gelei's evidence, the secondary split appears some time during pachytene. He also considered that the primary split remains open during pachytene. He seems to agree with the present writer on most of the happenings from leptotene till early diplotene.

Hence it may be assumed that the points summarized above will probably hold true for many or most other plants and animals which show usually no signs of marked differences in the reduction divisions from Dendrocoelum or Lilium.

SUMMARY

The chromomeres of liliaceous plants are usually better seen in smears than in sections.

The writer's observations show no longitudinal split in the leptotene stage.

The leptotene chromomeres are of different sizes.

Chromomeres of corresponding sizes are seen to synapse at zygotene.

At early pachytene, the average distance between the centers of chromomeres, in Lilium, is only two-thirds of that at late pachytene.

The leptotene threads in Lilium are about six and a half times as long as the first metaphase or anaphase chromosomes.

By special destaining, a minute dot has been demonstrated in each chromomere of early pachytene in Allium. This proves that the secondary split has not yet begun.

At late pachytene, most of the chromomeres showed a secondary split, not so clear as the primary split.

At late pachytene, in cells in Lilium which had the chromomeres further apart than usual, X's because of half-twists were seen in the connecting threads between some chromomeres.

In such cells there were seen a few chromomeres apparently without a partner.

Sometimes one chromomere was markedly larger than its partner.

Occasionally a pair of chromomeres was seen to be connected with another pair (usually of different size) by thick longitudinal threads instead of thin ones.

In Lilium and Fritillaria especially, a pair of minute chromomeres was sometimes seen, little or no thicker than the transverse threads connecting them.

At early diplotene, the chromomeres which separated at the primary split were observed to be of the same size in each pair.

The position of the genes at diaphase has been demonstrated, by the destaining method, in Aloë.

"Gene chromatin" and "extra chromatin" have been described and defined.

In different species (not polyploid) the amount of chromatin had no perceptible relation to the number of genes.

A modified hypothesis for crossing-over has been given.

LITERATURE CITED

Babcock, E. B., and Navashin, M.
1930. The genus Crepis. Bibl. Genetica, vol. 6, pp. 1–90.

Belar, K.
1929. Untersuchungen an den Staubfadenhaarzellen und Blattmeristemzellen von *Tradescantia virginica*. Zeitsch. f. Zellforsch., etc., vol. 10, pp. 73–134.

Belling, J.
1925. The structure of chromosomes. Brit. Jour. Exp. Biol., vol. 3, pp. 145–147.
1928*a*. A working hypothesis for segmental interchange between homologous chromosomes in flowering plants. Univ. Calif. Publ. Bot., vol. 14, pp. 283–291.
1928*b*. The ultimate chromomeres of Lilium and Aloë with regard to the numbers of genes. Univ. Calif. Publ. Bot., vol. 14, pp. 307–318.
1928*c*. Contraction of chromosomes during maturation divisions in Lilium and other plants. Univ. Calif. Publ. Bot., vol. 14, pp. 335–343.

Belling, J., and Blakeslee, A. F.
1922. The reduction division in haploid, diploid, triploid, and tetraploid Daturas. Proc. Nat. Acad. Sci., vol. 9, pp. 106–111.

Delaunay, L. N.
1926. Phylogenetische Chromosomenverkürzung. Zeitsch. f. Zellforsch., etc., vol. 4, pp. 338–364.

Gelei, J.
1921. Weitere Studien über die Oogenese des Dendrocoelum lacteum. . . . . Arch. f. Zellforsch., vol. 16, pp. 88–169.

Morgan, L. V.
1922. Non-crisscross inheritance in *Drosophila melanogaster*. Biol. Bull., vol. 42, pp. 267–274.

Muller, H. J.
1928. The measurement of gene mutation rate in Drosophila. . . . . Genetics, vol. 13, pp. 279–357.

Newton, W. C. F.
1927. Chromosome studies in Tulipa and some related genera. Linn. Soc. Jour. Bot., vol. 47, pp. 339–354.

Reuter, Enzio.
1930. Beiträge zu einer einheitlichen Auffassung gewisser Chromosomenfragen. . . . . Acta Zool. Fennica, vol. 9, pp. 1–487.

Sturtevant, A. H.
1926. A crossover reducer in Drosophila melanogaster, due to inversion of a section of the third chromosome. Biol. Zentralbl., vol. 46, pp. 697–702.

Sturtevant, A. H., and Dobzhansky, T.
1930. Reciprocal translocations in Drosophila, and their bearing on Oenothera cytology and genetics. Proc. Nat. Acad. Sci., vol. 16, pp. 533–536.

Wenrich, D. H.
1916. The spermatogenesis of Phrynotettix. . . . . Bull. Mus. Comp. Zool. Harvard, vol. 60, p. 57–135.
1917. Synapsis and chromosome organization in Chorthippus. . . . . Jour. Morph., vol. 29, pp. 471–516.

A TAXONOMIC STUDY OF POA BULBOSA L.

BY

MORRIS HALPERIN

University of California Publications in Botany
Volume 16, No. 6, pp. 171–183
Issued March 24, 1931

University of California Press
Berkeley, California

Cambridge University Press
London, England

A TAXONOMIC STUDY OF POA BULBOSA L.

BY

MORRIS HALPERIN*

The published taxonomic knowledge of *Poa bulbosa* L., i.e., of the normal (unproliferated) form, is limited entirely to European material. Inasmuch as the present study is the first to include both European and American material of *Poa bulbosa,* it has been possible to arrive at a broader familiarity with this form than was possible for the European investigators, working with European material only, and therefore to formulate a more comprehensive taxonomic description of the species than exists in the present literature.

Data as to the agrostologic differences between the normal form (*Poa bulbosa* L.) and the proliferated form (*Poa bulbosa* L. var. *vivipara* Koel.), as well as to the ecologic versatility of both of these forms, will be reported separately.

REVIEW AND CRITICISM OF THE LITERATURE

Poa bulbosa is a species named by Linnaeus. Linnaeus,[2] however, gives no adequate description nor do any of the authors whom he cites. Linnaeus mentions "Scheuch. Gram. 211" as one of the then existing descriptions of the grass in question. The reference is to Scheuchzer,[1] who uses the descriptive name "Gramen arvense, angustifolium, panicula, densa, foliacea, foliolis in panicula angustissimis," and follows this by a partial description of the leaves, panicle, and spikelets of the normal form. Koeler[3] cites Linnaeus[2] and quotes the phrase names employed by several pre-Linnaean naturalists. He distinguishes between the species and its proliferated variety. Mertens and Koch[5] give a description of both the normal and proliferous forms.

* Research Assistant in Agronomy, University of California, University Farm, Davis, California.

Desmazieres[4] and Kunth[6] give a very brief description of the normal form. Reichenbach[7] mentions Kunth,[6] essentially repeating the latter's description. Döll[8] gives a good description of the normal panicle and its parts.

Koch[9] observes that the panicle branches of the normal form occur solitary (a characteristic which is either denied or overlooked by several subsequent botanists). Hein[10] repeats the description of *Poa bulbosa* given by previous authors, but he gives also a description of the parts of the spikelet, reporting, for example, that the lemmas are indistinctly five-nerved. While not adding any original data, Boissier[11] gives a full description of the normal form, including all the characteristics noted by the previous authors.

Sowerby's[12] description of the normal form is excellent for its completeness, both of the vegetative and of the floral parts. He points out the first and only distinction found in the literature between the size and structure of the leaves and bulbs of the flowering stems and those of the barren shoots. This author noted also the venation on both the empty glumes and the flowering glumes and described the latter fully as to color, pubescence, and shape. Another valuable contribution made by Sowerby is that he gives actual dimensions for all structures which he describes. Bentham and Hooker[13] describe the panicle of the normal form in a manner almost identical with that of their British contemporary, Sowerby[12] just cited. However, the fact that Bentham and Hooker describe this form of *Poa bulbosa* as being "seldom above 6 inches high" and as having a panicle "not much above an inch long" indicates that they were acquainted with only exceptionally short and probably insufficient material. That their description is in accord, however, with their own material is evidenced by the illustrations in their companion volume prepared by Fitch and Smith.[14]

Schwarz[15] and Ascherson and Graebner[16] contribute only some quantitative data as to the size and color of the stems and leaves. The description given by Hegi[17] is virtually a copy of Ascherson and Graebner's.[16] Koch's[18] description is very brief and inadequate.

In a brief note on the utility of *Poa bulbosa* (presumably the proliferated form) for lawns in the South, Piper[19] states: "At Arlington Farm, Va., the grass flowers in April and May, some of the panicles normal, but in many the spikelets are proliferous. At Middleton, Conn., most of the panicles are normal." This is the first refer-

ence in the literature to the occurrence of normal spikelets of *Poa bulbosa* outside of Europe, and unfortunately includes no description or illustration of the material observed. Several years after the publication of this short note by Piper, Kennedy[20] reported what is doubtless the best contribution on *Poa bulbosa* in the recent literature. Kennedy, however, states: "All the specimens of *Poa bulbosa* found growing in the United States show complete proliferation of the spikelets," being evidently unaware of the above-quoted report by Piper.[19] Kennedy in discussing his discovery of the proliferous form in California and of its utilization on the Pacific Coast gives a description of the normal form of this grass, his description and illustrations being based on the two European specimens of normal *Poa bulbosa* then available in the herbarium of the Division of Agronomy, College of Agriculture, University of California at Berkeley. He did not consult additional European specimens available in other herbaria, with the result that the description is less complete than it otherwise might have been. Kennedy is the first investigator to describe the flowering structures other than the lemmas, his description of these, however, being very brief and incomplete. Halperin[21] reports the recent discovery of normal (unproliferated) florets in *Poa bulbosa* L. in the United States.

Perusal of the literature thus shows that the descriptions of *Poa bulbosa* L. (the normal form) in Europe are incomplete, and that this form in America has not been previously described. There is no mention of *Poa bulbosa* L. in any manual of North or South American grasses.

There is, moreover, considerable divergence in the descriptions presented by the various authors on certain points. The following examples will illustrate this:

The height of the normal plants is given variously as ranging between 9 cm. and 60 cm. The position of the stem is stated as being "always inclinate" in one of the quotations cited by Linnaeus,[2] "mostly geniculate at the base, then erect and somewhat inclined" by Koeler,[3] "erect, less often ascending" by Hegi,[17] and "erect" by Döll[8] and Boissier.[11] The shape of the panicle is referred to as "lax" by Desmazieres,[4] Mertens and Koch,[5] Kunth,[6] and Hegi,[17] and as "dense" or "compressed" by Scheuchzer,[1] Koeler,[3] Boissier,[11] and Schwarz.[15] The arrangement of the spikelets on the panicle is described as "spike-like or scarcely spreading" by Bentham and

Hooker,[13] as "rather open" by Koeler,[3] and as definitely "spreading" by Hein.[10] The length of the panicle is described as follows: "1–2 inches" by Koeler,[3] "2–4 cm." (¾–1½ inches) by Sowerby,[12] "2.5–5.0 cm." (1–2 inches) by Scheuchzer,[1] as "up to 8 cm." (3 inches) by Ascherson and Graebner[16] and by Koch.[18]

As to the number of panicle branches, there are partly contradictory statements in the literature: Scheuchzer[1] states that these occur in two's and three's, "never solitary"; Koeler[3] states that they occur in two's, "never in three's"; Reichenbach,[7] Koch,[9] Boissier,[11] and Koch,[18] agree that the panicle branches occur singly or in pairs; Sowerby[13] notes their occurrence in one's, two's, and three's; Mertens and Koch[5] and Kunth[6] report these as occurring only in pairs; and Hein[10] adds to the divergence of opinion by stating "Rispenaste zu zwei bis drei; untere Rispenaste zu *fünf* vorhanden" (the italics are inserted by the present writer). The pubescence on the panicle branches is mentioned only by Kunth,[6] Reichenbach,[7] Koch,[9] and Sowerby,[12] who describe it as scabrous, while Döll[8] on the contrary describes the branches as smooth. The length of the spikelets is reported by Sowerby[12] as being from 3 to 4 mm. (⅛ to 1/6 of an inch), but Ascherson and Graebner[16] and Koch[18] as well as Hegi[17] state that the spikelets are 6 mm. in length. The number of florets per spikelet in normal *Poa bulbosa* is reported upon by nearly all investigators. Several, including Kennedy,[20] mention a range of 3–6. Others variously report 4, 3–5, 4–6, 4–7, etc. Ascherson and Graebner[16] and Koch[18] report 4–6, seldom to 15 florets, per spikelet.

Thus, a comparison of the descriptions in the existing literature on *Poa bulbosa* shows numerous contradictory statements, these doubtless arising from the fact that the amount of material examined by each investigator was too small to permit a comprehensive knowledge of the variations in this form. Moreover, none of the preceding investigators give any information whatever on many points or else so little or such indefinite information as to be virtually negligible. The characteristics of *Poa bulbosa* L., i.e., normal *Poa bulbosa*, described either not at all or very inadequately in the literature are listed below:

Roots: number per plant; length; presence or absence of rootlets.

Bulbs: venation; lustre; width.

Stems: number per bulblet; shape; color; pubescence.

Nodes: number per culm; thickness relative to culm; location on culm.
Leaves: length; position relative to panicle.
Ligule: length; variation in size and shape.
Sheath: color; length; width; pubescence.
Blade: length; width; pubescence.
Panicle: color.
Panicle branches: length; color.
Pedicels: length; pubescence.
Palea: length; shape; pubescence.
Stamens: color; size of anthers.
Pistils: shape; color and length of ovary; length of stigma.
Caryopsis: presence or absence.
Lemma: length; relative prominence of keel.
Glumes: length; pubescence.

From a study of available American material, and by a comparison of this with European material, it was observed that the species is practically constant as to the characteristics listed above. It therefore seemed advisable to incorporate information concerning these in the revised taxonomic description of *Poa bulbosa* presented later in this paper.

COMPARISON OF THE CALIFORNIAN MATERIAL WITH THAT DESCRIBED IN THE EUROPEAN LITERATURE

There are several differences between the characteristics mentioned in the European literature and those of the Californian material mentioned by Halperin.[21] Chief among these differences are the following:

1. The Californian material is almost invariably about 50 cm. in length, viz., towards the upper limit designated for the height of the plant. This height is cited by most of the authors giving any figures as occurring seldom, most of the specimens being reported as 10–30 cm. in length.

2. The European material is described as being erect and less often ascending or geniculate, whereas all of the Californian material is distinctly geniculate, with the geniculation always occurring at the first node.

3. The European material is described as having the leaves mostly basal, the flowering stem being "leafless far below the panicle." The

Californian material shows leaves (blades and sheaths) to be present as much as one-half or more the length of the flowering culm from the base.

4. Five European authors describe the sheaths as being smooth; the others make neither any contradictory nor affirmative statement on this point. By contrast, the sheaths in nearly all of the Californian material are scabrous, at least on the margins.

5. Nearly all the European authors who make any statement as to the habit of the panicle on the culm describe it as "erect." The Californian material, in contrast, always has nodding and even one-sided panicles. Two of the earliest European authors, however, Linnaeus[2] in one of the citations which he quotes, and Koeler[3] observed the secund (one-sided) habit of the panicle.

6. The panicle branches are described in the European literature as being solitary, in two's, in three's, sometimes in five's, but chiefly solitary or in pairs. None of the Californian material has either one or two panicle branches, all being in three's, and in several cases, the lowermost groups are in four's.

7. The color of the panicle branches is mentioned by only four European authors, all of whom indicate it to be "red" or "purplish." Nearly all the Californian material contains panicle branches which are distinctly purple, but some of the branches are uncolored.

8. The European authors describe the lemma as "indistinctly 5-nerved." Most of the Californian material, however, shows five distinct nerves.

There are in addition a few minor differences between the European descriptions and those of the Californian material. These will not be mentioned here but will be included in the revised description of the species given below.

STUDY OF EUROPEAN SPECIMENS

The numerous omissions in the European literature describing *Poa bulbosa* L., and the many differences between the European descriptions and the observed characteristics of the Californian material, showed the desirability of examining some European material of normal *Poa bulbosa,* in a few accessible herbaria.

The specimens in the Herbarium of the University of California at Berkeley answer to the descriptions in the European literature in having the culm 10–30 cm. in length; basal leaves 3–8 cm. long; the panicle erect or virtually so; the panicle branches chiefly in two's or three's but also occasionally solitary, in four's or in five's; the panicle branches scabrous or puberbulent; and the lemma 3 mm. long. This material diverges from the European descriptions in having a definite geniculation at the lowermost node, only a few culms being erect; all the nodes, with rare exceptions, purple rather than brown; the sheath scabrous or scaberulous instead of smooth; the spikelets 4 mm. instead of 6 mm. in length; the number of florets 3–4 per spikelet rather than 4–6; the intermediate nerves of the lemma in many cases entirely distinct, instead of being always indistinct; and the lemmas entirely smooth in some cases, instead of being always densely pubescent.

The material from the Grass Herbarium of the United States National Museum is remarkably similar to the material just described from the Herbarium of the University of California. The statements in the preceding paragraph apply fully to the Grass Herbarium material.

The material in the Herbarium of the California Academy of Sciences is exceptional only in that one of the specimens, No. 100960, is only 8.5 cm. long.

The only available specimen of *Poa bulbosa* L. in the plant collection kept in the Division of Agronomy, College of Agriculture, University of California, Berkeley, is worthy of note as having exceptionally distinct pistils in regard to both ovaries and styles.

Below is a list of specimens of *Poa bulbosa* L. examined in connection with the writing of this paper. The following abbreviations are used to indicate the herbaria in which the specimens are located:

U.C. University of California, Berkeley.
U.C.X. Division of Agronomy, College of Agriculture, Berkeley.
U.S.N.M. Grass Herbarium, United States National Museum, Washington, D.C.
C.A.S. California Academy of Sciences, San Francisco.

Locality	Collector	Date	Herbarium number
AUSTRIA			
In siccis Austriae per Viennam	.....	.....	C.A.S. 100939
ENGLAND			
South Dene			
Yarmouth, P. I.	.....	.....	U.C. 329662
Yarmouth, Norfolk	A. M. Barnard 1329	May/40	U.C. 39562
FRANCE			
Coteaux arides de Saucours (Marne)	.....	24 Mai 1866	U.S.N.M. 294454
Coteaux Maritimes Cherbourg	L. Corbiere	6/5 1886	U.S.N.M. 947129
GERMANY			
Frankfurt A. M.	M. Durer	10 Mai 1899	U.C. 190377
Sachsenberg (Thuringen)	Fr. W. Martin	16.5 1869	U.S.N.M. 749261
Zittau, Saxony	Loscuz (?)	V. 1897	U.C.X. ——
GREECE			
Summit of (Mt.) Delphi in Euboeia	.....	.....	C.A.S. 100960
HUNGARY			
In collibus graminosis prope pagum Szent-Ivan	Dr. A. de Degen	1901 V. 8	U.C. 189548
Inter pagos Dubova et Plavisevitza	Dr. A. de Degen	V. 1904	U.S.N.M. 947127
LATAVIA			
Libau	.....	Juillet 1869	U.C. 76730
MOROCCO			
Xaŭen	Dr. Font Quer	1928	U.C. 383713
SWITZERLAND			
Sion-Kanton Wallis	.....	Mai 78	U.S.N.M. 947139
UNITED STATES			
Greenhouse in Washington, D. C. (?)	Hillman	.....	U.S.N.M. 734248
Raleigh, N. Carolina	B. W. Wells	May 1928	U.S.N.M. 1389746

Special mention must be made of the last two specimens listed above. These are American-grown material. U.S.N.M. specimen No. 734248 consists of one whole plant with a single flowering culm, all the spikelets being normal, except two which have a terminal bulbil. In the height of the plant and also as to the characters listed on pages 174–175, this specimen agrees completely with the Californian material. The other American specimen, U.S.N.M. No. 1389746, consists of one whole plant and two completely proliferated baseless culms. On the whole plant, the upper half of the panicle is completely proliferated, the lower half being nearly completely normal. In height, it is similar to the European rather than to the Californian material. In all other respects it agrees with the latter.

CONCLUSIOIN

All the foregoing data and discussion show that the present knowledge of *Poa bulbosa* L. is both defective and incomplete. The following comprehensive description of the normal form of *Poa bulbosa* is the result of an endeavor to correct and to expand the present information concerning this species, in order that there may be available as complete a description as the present knowledge of this form permits.

Poa bulbosa L.

Habit, perennial, tufted, geniculate at the lower node, 10–50 cm. in height; *roots,* fibrous, 5–10 from each bulblet, 1–3 cm. long, capillary, with numerous rootlets about 1 mm. in length; *bulblets,* about 0.5 cm. long, elliptic, at the base of the culm, crowded, brown, the sheaths scarious or papery with prominent veins; *culms,* one, erect above the lower node, usually gray green but often tinged with purple, cylindrical, about 1 mm. wide at the base and gradually narrowing toward the panicle, leafless (with exceptions) for at least one-third below the panicle, usually noticeably grooved, glabrous or often scaberulous; *nodes,* two on each culm, located (except very rarely) within the lowest third of the culm, purple, thickened but occasionally forming a groove in the culm; *leaves,* many, basal, 3–8 cm. long, rarely shorter or longer; *sheaths,* usually scabrous at least on the margins, completely surrounding the culm, nerves prominent, the sheaths of the basal leaves 1–4 cm. long and purple or purple tinged, those of the flowering culm 5–8 cm. long (rarely longer) and gray green or yellow generally tinged with purple; *blades,* puberbulent (seldom glabrous), those of the basal shoots 2–5 cm. long (rarely longer), those of the flowering stem up to 2 cm. (seldom to 4 cm.) long; *ligule,* white, hyaline, 1–3 mm. long, oblong or semi-circular,

entire or serrated; *panicle,* oblong-ovoid, one-sided, 1.5–5 cm. long; *panicle branches,* capillary, puberbulent, spreading during flowering, 3–10 mm. long (frequently longer), in two's or three's but the lowermost group in the panicle often in four's or five's; *pedicels,* 1–3 mm. long, puberbulent; *spikelets,* ovate-oblong, terminal on the branches or pedicels, 4–6 mm. long; *florets,* 3–6 (seldom more) per spikelet, compact; *glumes,* each with a prominent scabrous keel and with two lateral nerves, the lateral nerves often absent in the first glume, the first 2.5 mm. and the second 3 mm. in length; *lemma,* oblong-lanceolate, 3 mm. long, scarious, membraneous on the upper margins, acute, with a very prominent keel nearly always silky-hairy, and with 4 lateral nerves often very faint; *palea,* 2–5 mm. long, two-keeled, the keels scabrous and produced into two teeth; *stamens,* three, yellow, 1–1.5 mm. long, with filament about one-fourth as long as the anther; *pistil,* with a reddish brown round ovary 1 mm. long, and with two white, feathery stigmas 1 mm. long; *caryopsis,* absent.

SUMMARY

This report includes the first description of *Poa bulbosa* L. collected in the Western Hemisphere.

In connection with the taxonomic study of the Californian material of *Poa bulbosa,* a critical examination was made of the present (i.e., European) literature concerning this species. The existing literature shows several contradictions and numerous important defects in the extant knowledge of normal *Poa bulbosa.* To verify the herein reported variability and omissions in the European literature, a study of a number of European specimens of *Poa bulbosa* was made, and the discrepancies in the European descriptions as revealed by this study are described.

A detailed taxonomic comparison of the European and American material, describing the agrostological characteristics which distinguish them, is presented.

An extended description of *Poa bulbosa* L. including the European data, verified by additional European material, and including the modifications in the European descriptions necessitated by the material from America, is presented. This description includes approximately forty characteristics not mentioned by any of the preceding investigators but which the writer has found by studying both European and American material to be constant for the species.

ACKNOWLEDGMENTS

The writer expresses his gratitude for the use of the specimens which were obligingly made accessible to him by the various herbaria mentioned herein. Special thanks are gratefully expressed to Mrs. Agnes Chase, of the Grass Herbarium of the United States National Museum, for furnishing a few of the old European references mentioned in this paper, which would otherwise have been inaccessible, and for valuable criticism of the data presented in this paper. Mr. H. A. Schoth, Associate Agronomist of the United States Department of Agriculture, Corvallis, Oregon, and Mr. John Thomas Howell, Assistant Botanist, California Academy of Sciences, San Francisco, have been helpful in their critical reading of the manuscript.

LITERATURE CITED

[1] Scheuchzer, Joh.
1719. Agrostographia sive Graminum, Juncorum, Cyperorum, Cyperoidum, iisque affinium Historia, pp. 211–212 and pp. 242–243, tab. IV, fig 13 (Tiguri).

[2] Linnaeus, C.
1753. Species Plantarum, Tomus I, p. 70.

[3] Koeler, Georgius Ludovicus.
1802. Descriptio Graminum in Gallia et Germania, p. 189 (Francofurti ad Moenum).

[4] Desmazieres, J. B. H. J.
1812. Agrostographie des Departements du Nord de la France, p. 83 (Lille).

[5] Mertens, Franz Carl, und Koch, Wilhelm Daniel Joseph.
1823. J. C. Rohlings Deutschlands Flora, Erster Band, p. 609 (Frankfurt am Main).

[6] Kunth, Carolus Sigismundus.
1833. Agrostographia Synoptica sive Enumeratio Graminearum, Tomus primus, p. 352.

[7] Reichenbach, Ludovicus.
1850. Agrostographia Germanica sistens Icones Graminearum (editio secunda; Leipzig), p. 49.

[8] Döll, J. Ch.
1855. Flora des Grossherzogthums Baden, p. 175 (Carlsruhe).

[9] Koch, D. Guil. Dan. Jos.
1857. Synopsis Florae Germanicae et Helvetiae (editio tertia), Para prima, pp. 696–697.

[10] Hein, Heinrich.
1877. Graeserflora von Nord- und Mittel-Deutschland, p. 89 (Weimar).

[11] Boissier, Edmond.
1884. Flora Orientalis, volumen quintum, pp. 605–606.

[12] Sowerby, John Edward.
1886. English Botany (ed. 3; London), vol. 11, Gramina, pp. 112–114.

[13] Bentham, Geo., and Hooker, J. D.
1887. Handbook of the British Flora (ed. 5; London), p. 540.

[14] Fitch, W. H., and Smith, W. C.
1887. Illustrations of the British flora (ed. 2; London), fig. 1246.

[15] Schwarz, August Friedrich.
1892. Flora der Ungegend von Nürnberg-Erlangen, p. 832 (Nürnberg).

[16] Ascherson, Paul, und Graebner, Paul.
1898–1902. Synopsis der Mitteleuropaischen Flora, Zweiter Band, p. 392 (Leipzig).

[17] Hegi, Gustav.
1907. Illustrierte Flora von Mittel-Europa, Band I, pp. 300–308 (München).

[18] Koch, W. Dan. Jos.
1907. Synopsis Deutscher und Schweizer Flora, vol. 3, pp. 2752–2753.

[19] Piper, C. V.
1924. Bulbous Bluegrass (*Poa bulbosa* L.), Torreya, vol. 24, pp. 7–8 (Jan.–Feb.).

[20] Kennedy, P. B.
1929. Proliferation in *Poa bulbosa*, Jour. Am. Soc. Agron., vol. 21, pp. 80–91 (January).

[21] Halperin, Morris.
1931. The Occurrence of Normal (Unproliferated) Florets in *Poa bulbosa* in the United States, Jour. Am. Soc. Agron., vol. 23, No. 7 (July).

NOTES ON LAURENCIA, WITH SPECIAL REFERENCE TO THE JAPANESE SPECIES

BY

YUKIO YAMADA

University of California Publications in Botany
Volume 16, No. 7, pp. 185–310, plates 1–30, 20 figures in text
Issued June 26, 1931

University of California Press
Berkeley, California

Cambridge University Press
London, England

NOTES ON LAURENCIA, WITH SPECIAL REFERENCE TO THE JAPANESE SPECIES

BY

YUKIO YAMADA

The genus *Laurencia* was founded by Lamouroux in 1813. He enumerated eight species and ten "*spec. ineditae,*" most of them having been removed from the genus *Fucus* in the earlier usage. Although he did not designate a type species, *L. pinnatifida* may be assumed as one. Since that time, several authors have added new species to the genus or removed others from this genus to other genera. Among these authors the names of Harvey, Montagne, Lenormand, and Kützing may be mentioned.

The first systematic arrangement was attempted by J. G. Agardh in his *Species genera et ordines algarum,* vol. 2, which appeared in 1863 and this was revised by him in his "*Epicrisis*" in 1876. Since then, many additional species have been described but no one has attempted to elucidate this troublesome genus systematically; the above mentioned system of J. Agardh is, of course, not a complete one.

From the morphological point of view, the works of Falkenberg and Kylin must be mentioned; the former studied especially the structure of the frond, while Kylin cleared up much about the structure of the frond as well as the reproductive organs.

While working on the marine algae from the Orient in the herbarium of the University of California under the guidance of Professor W. A. Setchell and Professor N. L. Gardner in 1928, I had the opportunity to study the Japanese species of this genus. On the Japanese coasts, from Hokkaido, the northern island of Japan, to Formosa and also to the Micronesian Islands under Japanese mandatory rule, there are several species of this genus. Because of the fact that the external habit of the frond as well as the stichidial branchlets are very variable according to the conditions under which they grow, it has been nearly impossible for us to determine our species exactly. At the suggestion of Professor Setchell, therefore, I started to study this difficult matter in Berkeley, but to carry the work through successfully it became necessary to examine authentic specimens of all described species. Very fortunately, since leaving California in March 1929, I have had a very favorable opportunity to visit almost all the important herbaria in America as well as in Europe so far as the

phycological study is concerned, in order to study these types, etc., and have examined as many authentic specimens as possible.

The Japanese material used for the present study consists of specimens belonging to the Tokyo Imperial University which includes the specimens of the late Professor K. Yendo, the herbarium of Dr. K. Okamura, and my own collection. I wish to express my most cordial thanks to Professor W. A. Setchell of the University of California, under whose guidance the present work was carried out, and also to Professor N. L. Gardner of the same University, who gave me most valuable suggestions during my stay in Berkeley, and also to both for their kindness in allowing me to use all specimens and books in their possession. My sincere thanks are also due to my teachers, Professor B. Hayata of the Tokyo Imperial University, who allowed me to bring specimens from the first mentioned collection abroad with me; and to Dr. K. Okamura, Director of the Imperial Fisheries Institute, Tokyo, who gave me permission to examine his herbarium, for their kind permissions and also for their kind encouragements.

And now it is my pleasant duty to express my sincere appreciation to the savants of several universities and herbaria who kindly allowed me to examine specimens and also gave me valuable suggestions: Dr. A. D. Cotton and Miss I. O. Dickinson in the herbarium of the Royal Botanic Gardens, Kew; Professor L. Diels, Professor R. Pilger, and Dr. O. C. Schmidt in the Botanical Museum, Berlin-Dahlem; Professor H. H. Dixon and Mr. J. Murray, Trinity College, Dublin; Dr. W. A. Goddijn of the Herbarium of Leyden; Dr. M. A. Howe of the New York Botanical Gardens; Dr. K. Keissler of the Natural History Museum, Vienna; Professor L. Mangin, Dr. G. Hamel, and Mr. R. Lami of the National Museum of Natural History, Paris; Professor S. Muerbeck and Professor H. Kylin of the University of Lund; Dr. A. B. Rendle, Mr. A. E. Gepp, and Mr. G. Tandy in the British Museum, Natural History, London; Professor F. Kolderup-Rosenvinge, Dr. F. Börgesen and Dr. H. Petersen of the University of Copenhagen; Professor W. Smith and Dr. W. E. Evans of the Royal Botanic Gardens, Edinburgh; Professor W. Stiles of the University of Birmingham; Professor N. Svedelius of the University of Upsala; Professor R. Thaxter and Dr. C. W. Dodge of the Farlow Herbarium of Harvard University, Cambridge, Massachusetts; Professor W. R. Taylor of the University of Pennsylvania; Professor J. E. Tilden of the University of Minnesota; Professor R. Viguier of the University of Caen; and Dr. Anna Weber-van Bosse at Eerbeek, Holland.

AN ANALYTICAL KEY TO THE SPECIES OF *LAURENCIA*

Surface cells elongated radially and arranged like palisade cells in the cross-section of branchlets ..... Sect. **Palisadae**

Branches and branchlets covered very densely sooner or later with very short wart-like ultimate branchlets.

When young, branchlets very loose, only in age covered densely with wart-like branchlets ..... **L. intermedia** Yamada

Even when young, branches covered with wart-like branchlets. **L. papillosa** Grev.

Branches and branchlets not as above, ultimate branchlets disposed loosely.

Branches and branchlets very few ..... **L. flagellifera** J. Ag.

Branches and branchlets abundant.

Branches often curved, branchlets often secund, frond small. **L. perforata** Mont.

Branches and branchlets not as above.

Ultimate branchlets very short ..... **L. paniculata** J. Ag.

Ultimate branchlets not very short.

Branches pinnate.

Frond cartilaginous ..... **L. cruciata** Harv.

Frond not as above ..... **L. palisada** Yamada

Branches not pinnate ..... **L. corallopsis** Howe

Surface cells neither elongated radially nor arranged like palisade cells in the cross-section of branchlets.

Frond not clearly compressed.

Lenticular thickening abundant in the walls of the medullary cells. Sect. **Fosterianae**

Plants small.

Surface cells projecting near the end of branchlets.

Basal part cushion-like ..... **L. pannosa** Zanard.

Basal part loosely entangled ..... **L. mariannensis** Yamada

Surface cells not projecting.

Fronds decumbent or at least the basal part decumbent.

Plants very small ..... **L. pygmaea** Web. van Boss.

Plants not so small as above.

Branchlets often virgate.

Plants thick ..... **L. venusta** Yamada

Plants slender ..... **L. nidifica** J. Ag.

Branches not virgate ..... **L. radicans** Kg.

Fronds erect.

With the percurrent axis ..... **L. microcladia** Kg.

Without the percurrent axis ..... **L. indica** Hauck.

Plants large.

Fronds with the percurrent axis.

Branches nearly distichous ..... **L. japonica** Yamada

Branches not as above.

Frond often becoming very large.
Color often reddish ..... **L. virgata** J. Ag.
Color often yellowish ..... **L. nipponica** Yamada
Color often blueish ..... **L. obtusiuscula** Set. et Gardn.
Fronds not so large as above.
Branches often virgate.
Fronds slender ..... **L. Johnstonii** Set. et Gardn.
Fronds not as above ..... **L. Okamurai** Yamada
Branches not virgate.
Color blackish ..... **L. coronopus** J. Ag.
Color yellowish red..... **L. Masonii** var. **orientalis** Yamada

Fronds without percurrent axis.
Fronds very slender ..... **L. gracilis** Hook. et Harv.
Fronds not so slender as above.
Branches often fastigiate ..... **L. scoparia** J. Ag.
Branches not as above ..... **L. Fosteri** Grev.

Lenticular thickenings absent or, if any, very few in the walls of the medullary cells ..... Sect. **Cartilagineae**

Stichidial branchlets compound.
Fronds cartilaginous.
Plants very large, stout ..... **L. tasmanica** Harv.
Plants not as above.
With percurrent axis.
Frond slightly compressed..... **L. distichophylla** J. Ag.
Frond cylindrical ..... **L. regia** Harv.
Without percurrent axis ..... **L. corymbosa** J. Ag.
Frond not cartilaginous.
With percurrent axis.
Clusters of the stichidial branchlets arranged spirally.
L. Yendoi Yamada
Clusters of the stichidial branchlets not as above.
L. composita Yamada
Without percurrent axis ..... **L. heteroclada** Harv.

Stichidial branchlets simple.
Fronds small or delicate.
Fronds dwarf.
Branches claviform ..... **L. claviformis** Börg.
Branches not as above ..... **L. nana** Howe
Fronds not dwarf, but slender.
Branches fastigiate ..... **L. brachyclados** Pilg.
Branches not as above ..... **L. chondrioides** Börg.
Fronds large and stout.
Fronds cartilaginous.
Short branches very few in number ..... **L. Casuarina** J. Ag.
Short branches numerous
Ultimate branchlets very short and wart-like.
Ultimate branchlets only in the upper part of branches.
L. botryoides Gaill.
Ultimate branchlets not as above.
Fronds slightly compressed..**L. cartilaginea** Yamada
Fronds cylindrical ..... **L. rigida** J. Ag.

Ultimate branchlets not very short as above, not wart-like.
Branches long, loosely disposed ..... **L. flexilis** Setch.
Branches not so long as above, densely disposed.
L. tropica Yamada

Fronds not cartilaginous.
Fronds with percurrent axis.
Branches nearly distichous ..... **L. hybrida** Lenorm.
Branches not as above.
Ultimate branchlets very small.
Ultimate branchlets spine-like.. **L. seticulosa** Grev.
Ultimate branchlets wart-like.
L. glandulifera Kg.
Ultimate branchlets not so small as above.
Ultimate branchlets capitate.. **L. capituliformis** Yam.
Ultimate branchlets clavate ..... **L. obtusa** Lamx.
Fronds without percurrent axis.
Fronds often slightly compressed ..... **L. Poitei** Howe
Fronds cylindrical.
Often provided with curved branches.
L. subopposita Setch.
Without curved branches.
Branchlets very soft ..... **L. clavata** Sonder.
Branchlets not very soft.
Frond slender ..... **L. filiformis** Mont.
Frond not as above.
L. chilensis De Toni, Forti et Howe

Frond clearly compressed ..... Sect. **Pinnatifidae**
Lenticular thickenings present, at least in the basal part of the frond.
Thallus creeping ..... **L. sinicola** Setch. et Gardn.
Thallus not as above.
Color often blackish.
Fronds very strongly compressed ..... **L. pinnatifida** Lamx.
Fronds not so strongly compressed as above.. **L. thyrsifera** J. Ag.
Color not blackish, often yellowish or red.
Branches often costate, at least near the base of the frond.
L. Brongniartii J. Ag.
Branches not as above ..... **L. elata** Harv.
Lenticular thickenings absent.
Surface cells projecting near the end of branchlets.... **L. pinnata** Yamada
Surface cells not as above.
Margins of the fertile branches undulate.
Fronds large and stout ..... **L. undulata** Yamada
Frond not so large and stout as above.... **L. botrychioides** Harv.
Margins of the fertile branches not undulate.
Plants small ..... **L. ceylanica** J. Ag.
Plants large.
Fronds soft, color vividly red ..... **L. Grevilleana** Harv.
Fronds and color not as above..... **L. spectabilis** Post. et Rupr.

Section Palisadae

Frond almost always cylindrical, surface cells elongated radially and arranged like palisade cells in the cross-section of branchlets; no lenticular thickenings in the walls of the medullary cells.

The present section appears to represent a well limited group, all species belonging to the present section showing the radially elongated surface cells in the cross-section of branchlets which are arranged like the palisade cells. The frond is, in most species, fleshy and deeply tinted, some being black in the dried state, though the color may be changed sometimes according to the conditions under which they grow. In the walls of the medullary cells, I have never found any lenticular thickenings. They are mostly distributed in warm waters.

Laurencia papillosa (Forskaal) Greville

Plate 1, figures *a*, *b*

Alg. brit. syn., p. lii; J. Agardh, Spec. alg., vol. 2, p. 756; Epicr., p. 652; Kützing, Tab. phyc., vol. 15, pl. 62; De Toni, Syll. alg., vol. 4, p. 789.

Fucus papillosus Forskaal, Flor. Aeg. Arab., p. 190.

Fucus thyrsoides Turner, Hist. Fuc., pl. 19.

Laurencia cyanosperma Lamouroux, Ess. sur gen. de fam. des thalas., p. 42.

Type locality.—Red Sea.

In the herbarium of Forskaal now preserved in the Botanical Museum in Copenhagen, there is the type specimen of this species, which was collected by Forskaal himself in 1763 in "Mar. rub. ad Mockham." In this specimen the frond is 5.5 cm. high, cartilaginous, irregularly branched, and covered very densely with small tuberculate branchlets. The surface cells are very strongly elongated radially in the cross-section of branchlets and arranged like palisade cells; in the surface view they are not projecting; cell walls very thick. There are no lenticular thickenings present in the walls of the medullary cells.

In the Agardhian herbarium as well as in the herbarium of the Royal Botanic Gardens, Kew, there are preserved several specimens from the same source as the type, which show exactly the same characteristics as the specimen in Copenhagen.

At Caen, I have studied Lamouroux's specimen of *L. cyanosperma* Lamx. This specimen is most probably referable to the present species, showing the characteristics of *Palisadae* in the shape and arrangement of the surface cells in the cross-section of branchlets. On the other

hand, most of Kützing's specimens under *L. cyanosperma* Lamx. found in the herbarium of the Botanical Museum in Berlin and at Eerbeek, do not seem to be the same as the above mentioned Lamouroux's specimen, although they are not uniform.

De Toni referred *L. oophora* Kg. to the present species, although with a question mark. I have studied the specimen of Kützing at Eerbeek and found that this species does not show any characteristic of the *Palisadae* and is, most probably, a form of *L. obtusa* Lamx.

Laurencia intermedia sp. nov.

Plate 1, figure *c*; plate 2

Fronde 20 cm. alta, 1–2 mm. crassa, cylindrica, caespitosa, plerumque ramo principale percurrenti; ramulis paniculatis, quoquoversum egredientibus, deinde ramulis ultimis verrucaeformibus dense obtectis; cellulis superficialibus in sectione transversa evidenter radiatim elongatis, 32–39μ longis, 10–16μ latis, simili modo ut cellulis valliformibus dispositis; cellulis medullaribus partem incrassatam lenticulatam ad parietem non ostendentibus; stichidiis ramulis ultimis sterilibus conformibus; cystocarpiis et antheridiis ignotis.

Habitat.—Enoshima, Province Sagami, Japan.

Frond up to 20 cm. high, 1–2 mm. thick, cylindrical, caespitose, usually with a principal percurrent axis, paniculately branched; branches in every direction; ultimate branchlets clavate, truncate at apices when young, but in age branches and branchlets covered with small wart-like branchlets densely; surface cells clearly elongated radially in the cross-section of branchlets, about 32–39μ long, 10–16μ wide, arranged like palisade cells, in the surface view not projecting; there are no lenticular thickenings in the walls of the medullary cells; stichidia are like the ultimate sterile branchlets; cystocarps and antheridia unknown.

Some specimens of the present species have been distributed by Okamura as No. 20 of his Alg. Exs. Jap. under the name of *L. dendroidea* J. Ag., but this name is evidently not correct as he himself recognized later (cf. Nippon Sorui Meii, 2d ed., p. 68). It belongs to the *Palisadae,* as the above description shows, and comes most nearly to *L. paniculata* J. Ag. on the one hand, and *L. papillosa* Grev. on the other; in the young stage the branchlets being loosely disposed, thus showing a strong resemblance to *L. paniculata* J. Ag., while when it becomes older, branches and branchlets are covered densely with small wart-like ultimate branchlets showing some likeness to *L. papillosa* Grev.

Although I have described here our specimens as a new species, separating it from both *L. paniculata* J. Ag. and *L. papillosa* Grev.,

I am not without doubt as to whether these two species may not be the same and their type specimens representing the extreme forms of one very variable species in which *L. intermedia* may be included.

Laurencia paniculata (Agardh) J. Agardh

Plate 3, figure *a*

Spec. alg., vol. 2, p. 755; Epicr., p. 651; De Toni, *l.c.*, p. 788.
Chondria obtusa var. *paniculata* Agardh, Spec. alg., p. 343.
Laurencia thuyoides Kützing, Tab. phyc., vol. 15, p. 26, pl. 74, figs. *a*, *b*.

Type locality.—Adriatic Sea.

In the herbarium of J. G. Agardh, in the cover of this species, there are seven sheets and some unmounted specimens, among which Nos. 36701, 36711 and 36716 are from the herbarium of C. Agardh. The first number is "ex Gadibus Cabrera in Hb. Ag.," while the second is from "Triest, in Hb. C. Ag.," and the last is most probably the same as the second. Therefore, No. 36711 should be taken as the type of *Chondria obtusa* var. *paniculata* Ag. on which J. Agardh's *L. paniculata* was founded, though it is not clear whether it was collected by Hoppe and Hornschuch as reported in the original description of C. Agardh. This number consists of two specimens, about 5 and 5.5 cm. high respectively, with fronds rather thick in comparison with their length. But these two specimens appear to me to be quite different specifically, one from the other. In the specimen on the right, the frond is coarser than in the other, and the surface cells are elongated radially and disposed like palisade cells in the cross-section of branchlets while in the left specimen, they are not so arranged. In No. 36716 the structure is the same as in the left specimen. Number 36701 is also composed of two specimens and they are larger and coarser than those of No. 36711, being about 9–11 cm. high, paniculate-pinnate in branching, branching not dense, ultimate branchlets very short, wart-like but disposed very loosely, being quite different from those in the type of *L. papillosa* Grev. In anatomical structure, these specimens show characteristics of the *Palisadae* very clearly and appear to be the same as the right specimen in No. 36711.

On the other hand, in the herbaria of Dr. Weber-van Bosse and that of the Botanical Museum, Berlin-Dahlem, there are some specimens of *L. glandulifera* Kg. which originally belonged to the herbarium of Kützing; among them one, kept in Berlin-Dahlem, was figured by Kützing in his Tabulae phycologicae, vol. 15, pl. 59, *c*, *d*. These

specimens appear to me to be exactly the same as the left specimen of No. 36711 in the herbarium at Lund. And so, taking the right specimen of this number in the Agardhian herbarium as the type of *L. paniculata* J. Agardh, the left specimen of the same number as well as the Kützing specimens must be separated from *L. paniculata* J. Ag. as *L. glandulifera* Kg., an independent species.

Kützing also described a new species of *Laurencia* from New Caledonia, calling it *L. thuyoides* Kg. Its type specimen was collected by Vieillard and figured by Kützing in Tabulae phycologicae. It is preserved now at Eerbeek, in the herbarium of Kützing, the property of Dr. Weber-van Bosse. By her kind permission I have examined it and have come to the conclusion that it is referable to *L. paniculata* J. Ag., the shape and the arrangement of the surface cells coinciding well with those of J. Agardh's species in question.

From the Malay archipelago Weber-van Bosse reported a new form of this species, naming it *L. paniculata* f. *Snackeyi* Weber-van Bosse, I have been allowed by her to examine the type at Eerbeek. To me, however, it appears to be more reasonable to place this form under *L. obtusa* Lamx. than under *L. paniculata* J. Ag., because it shows no trace of the characteristics of the *Palisadae*. This form seems to be distributed rather commonly, because I have also personally found it in the Palao Islands of the tropical Pacific.

Okamura's Alg. Exs. Jap. No. 20 under the name of *L. dendroidea* J. Ag. comes near the present species, but as I consider it to be different specifically from J. Agardh's *L. paniculata,* I have described it as a distinct species.

Laurencia perforata (Bory) Montagne

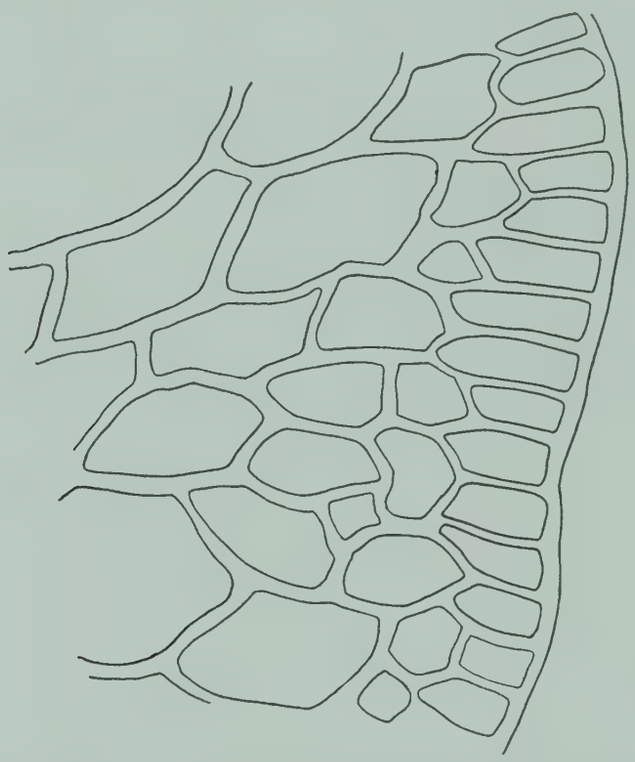
Plate 3, figure *b*; figures A, B

Flor. Canar., p. 155; Kützing, Tab. phyc., vol. 15, pl. 49; J. Agardh, Spec. alg., vol. 2, p. 748; Epicr., p. 648; De Toni, *l.c.*, p. 784.
Fucus perforatus Bory, Essai sur les isles Fort., p. 503, pl. 5, fig. 1.
Laurencia vaga Kützing, Tab. phyc., vol. 15, p. 18, pl. 50; De Toni, *l.c.*, p. 8.

Type locality.—The Canary Islands.

In the cover of *L. perforata* Mont. of the Thuret herbarium, Paris, is the type of *Fucus perforatus* Bory. This sheet contains five specimens numbered from 1 to 5, and is accompanied by a colored figure and the manuscript of the description, which correspond to the figure and the description of Bory, above cited. On the label accompanying

this figure and manuscript is a note of Thuret, reading: "*Gigartina perforata* J. Ag. Sp. Alg. p. 749. Les échantillons 1, 4 et 5 sont les *Gigartina pistillata* jeune. Les nos. 2 et 3 sont le *Laurencia.*" I have examined the anatomical characters of No. 3. The surface cells are elongated radially and disposed evidently like palisade cells in the cross-section of branchlets, not projecting in the surface view; there are no lenticular thickenings in the walls of the medullary cells.



A. *L. perforata* Mont. (= *Fucus perforatus* Bory). The type specimen. × ca. 330. A cross-section of a branchlet.

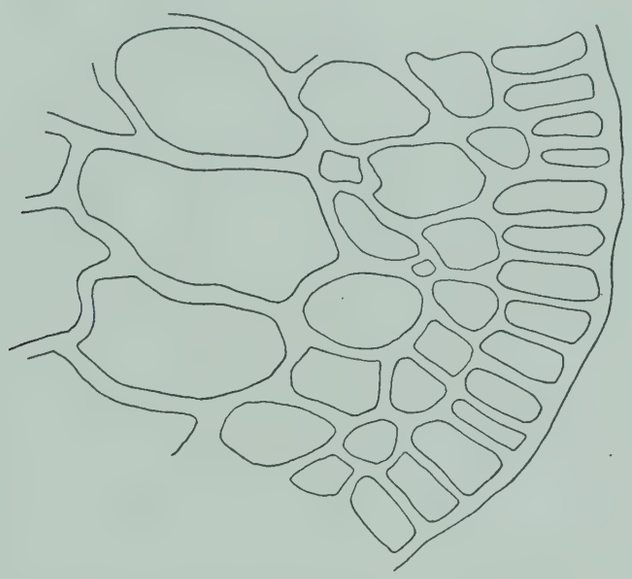
As the above cited work of Bory is rather rare, it does not seem to me to be superfluous to quote from his manuscript.

Fucus ramosus, ramis teretibus, recurvatis, intricatis, crassiusculis; ramulis angulis rectis, brevibus, truncato-perforatis extremitate, ore subdentato. Formant des couches très entremelées, comme verruqueuses brunes. Tige droite, rameaux partout souvent du meme endroit en divergeant ou fourchus, ronds, charnus; petits rameaux insérés en dessus, montant, formant des angles droites avec le gros rameau qui les porte, comme tronqués à leur extrémité qui est perforée et munie d'espèces de crénélures.

In the herbarium of Montagne there are also several specimens from the type locality under *L. perforata* which agree well with Kützing's figures. They are more slender and more decumbent than the type of Bory but seem to be referable to the same species as Bory's type. Bory's type shows some resemblance to the type of *L. paniculata* J. Ag. in general habit as well as in anatomical structure. C.

Wright's specimens from Loo-choo, collected in the North Pacific Exploring Expedition and determined by Harvey as *L. perforata* Mont., are preserved in several herbaria. They do not appear to be uniform and some are the young form of *L. flexilis* Setch. or *L. tropica* Yam.

Kützing described a new species, *L. vaga* from New Caledonia and gave figures of it in Tabulae phycologicae. I have examined a specimen, undoubtedly a cotype, collected by Vieillard in New Caledonia, in Paris. The anatomical characters of this specimen are the same as those of *L. perforata* Mont., so J. Agardh was probably correct when he put this species of Kützing into the synonymy of the present species.



B. *L. vaga* Kg. Cotype specimen in Paris. × ca. 330.
A cross-section of a branch.

The type specimen of *L. decumbens* Kg. is preserved in the herbarium of Kützing in Eerbeek. In external appearance it shows considerable resemblance to *L. perforata* Mont. although the frond is more slender than in the Montagne specimens with which the present species has been already compared by J. Agardh in the Epicrisis. The anatomical structure of the type specimen, shows, however, that it is far from being *L. perforata* Mont. because it lacks the character of the *Palisadae*. But because Kützing's species is represented by only one sterile specimen, it is very difficult to obtain an exact idea of it.

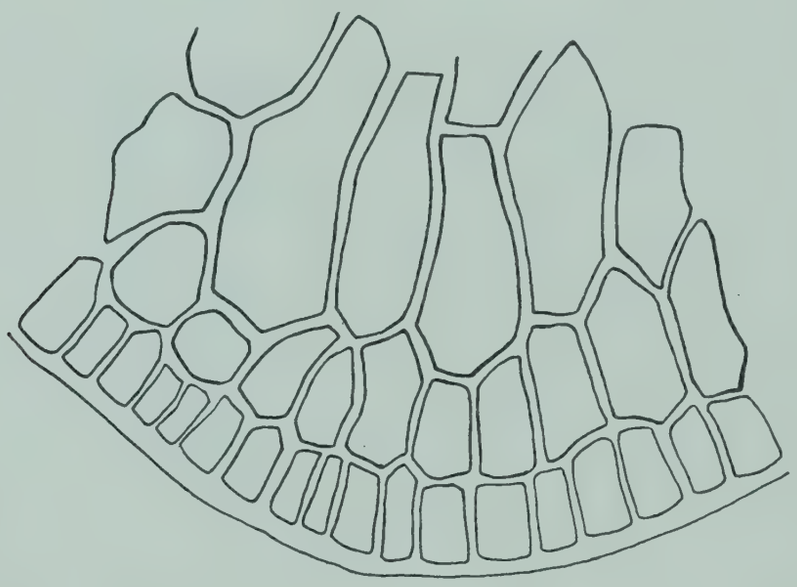
Numbers 794 and 1889 of the Phycolotheca Boreali Americana, distributed under the name of the present species, are certainly not *L. perforata* Mont., at least in the copies preserved in the herbarium of the Natural History Museum in Vienna. Even generically the

determination does not seem to me to be correct. I wonder whether we may have here some member of *Rhodymeniaceae,* although I can not state with any certainty as to its exact nature.[1]

Laurencia palisada sp. nov.

Plate 4, figure *a*; figures C, D

Radice non fibrosa; fronde 6.5 cm. alta, leviter compressa, non rigida, ad basin 2–3 mm. crassa, sursum mox in ramos primarios decomposita; ramis primariis enormiter bi- tripinnatim ramosis, saepe distichis; ramulis minoribus patentibus, in partem superiorem plerumque ramulis ultimis dense obtectis; ramulis ultimis clavatis, ad apicem



C. *L. palisada* sp. nov. The type specimen. × ca. 250.
A cross-section of a branchlet.

plerumque capitatis vel tuberculis parvis verrucaeformibus ornatis; cellulis superficialibus in sectione transversa radiatim elongatis, 26–40μ longis, 10–13μ latis, simili modo ut cellulis valliformibus dispositis; cellulis medullaribus partem incrassatam lenticulatam ad parietem non ostendentibus; antheridiis fasciculos ramosos formantibus, axibis ramorum fasciculorum in cellulam pyriformem magnam terminatis, cellulis terminalibus 20–32μ longis, 12–23μ latis; spermatiis oblongis 5.2–6.5μ longis, 2.5–4.0μ latis; colore sicco fusco-purpureo.

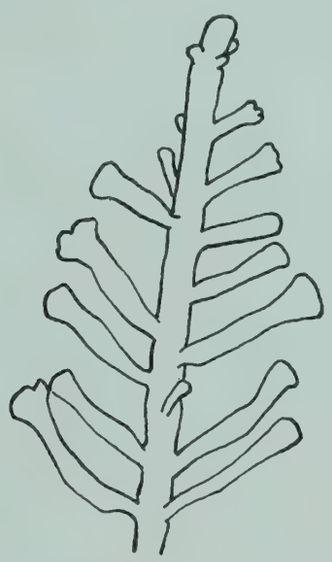
Habitat.—Kōtōshō (S. Sasaki), Takao (in Herb. Kew), Formosa.

Root not fibrous; frond about 6.5 cm. high, slightly compressed, not so rigid, 2–3 mm. thick at the base, soon being divided into some primary branches; primary branches pinnately ramified, often distichous, usually closely covered with branchlets in the upper part, open, branches again pinnately set with many ultimate branchlets; ultimate branchlets clavate, mostly capitate or provided with small

[1] Cf. M. A. Howe, in N. L. Britton, Flora of Bermuda, p. 519, 1918.—Editor.

wart-like protuberances; surface cells radially elongated in the cross-section of branchlets, 26–40μ long, 10–13μ broad, no lenticular thickenings present in the walls of the medullary cells; antheridia forming branching clusters, each surrounding an axis which ends in a pyriform cell being 20–32μ long, 12–23μ broad; spermatia about 5.2–6.5μ long, 2.5–4.0μ broad. Color blackish purple on drying.

There are four specimens in the herbarium of the Royal Botanic Gardens, Kew, under the name of *L. papillosa* Grev. which were collected by Seinhoe at Takao, Formosa. They are all referable to the present species.



D. *L. palisada* sp. nov. A small branch. × 3.5.

Laurencia flagellifera J. Agardh

Plate 4, figure *b*

Spec. alg., vol. 2, p. 747, Epicr., p. 648; De Toni, *l.c.*, p. 782.

Type locality.—East Indies.

In the Agardhian herbarium, there are three numbers in the cover of the present species: 36604–36606, being most probably of one and the same origin: "Sub no. 168 Wight. x India orient. miss-ded. Hooker." So they represent the type, and are about 9–13 cm. long, nearly black in color, provided with very few branchlets.

The surface cells are elongated radially and arranged like palisade cells in the cross-section of branches, not projecting in surface view; there are no lenticular thickenings in the walls of the medullary cells.

J. Agardh included the present species in his *Filiformes,* placing it next to *L. heteroclada* Harv., but this does not seem to me to be preferable. From the character of the surface cells, this species must be grouped together with *L. papillosa* Grev., etc.

According to Yendo (Notes on algae new to Japan, VI, p. 90) the present species as well as *L. paniculata* J. Ag., are related closely to *L. heteroclada* Harv., *L. corymbosa* J. Ag., *L. tasmanica* Harv., etc., but that is only in the superficial, external appearance and, I think, there is clear distinction between the group of *L. paniculata* J. Ag. and that of *L. corymbosa* J. Ag., etc., as mentioned above.

Laurencia corallopsis (Montagne) Howe

Britton, Flora Bermuda, p. 519; Britton and Millspaugh, Bahama Flora, p. 566; De Toni, *l.c.*, vol. 6, p. 370.

Sphaerococcus corallopsis Montagne. Hist. cub. bot., pl. cell., p. 47; Ic. flor. cub., pl. 3, fig. 1.

Laurencia cervicornis Harvey, Ner. bor. amer., vol. 2, p. 73, pl. 18, *c*.

Type locality.—Near Havana, Cuba.

In the herbarium Montagne in Paris, the type specimen of *Sphaerococcus corallopsis* Mont. which was delineated by Montagne, is preserved. As to the anatomical structure of the type specimen, there are no lenticular thickenings in the walls of the medullary cells; the surface cells are not projecting in the surface view, even near the top of the ultimate branchlets, are elongated radially in the cross-section and arranged like palisade cells, but not so strongly as figured by Montagne.

Howe placed *L. cervicornis* Harv. in the synonymy of the present species. I have also examined Harvey's type of that species at Dublin, and have come to the same conclusion as that of this careful phycologist of New York.

Laurencia cruciata Harvey

Plate 5, figure *a*; figure E

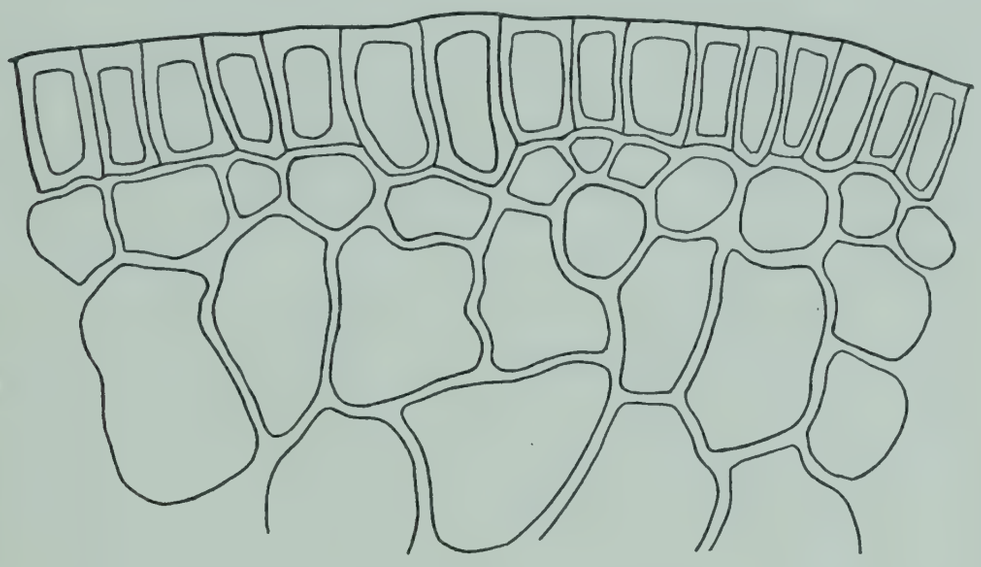
Acc. of mar. bot. of colony of West Austr. Trans. Irish Acad., vol. 22, p. 544; Phyc. aust. syn., no. 311; J. Agardh, Epicr., p. 652; De Toni, *l.c.*, p. 790.

Type locality.—West Australia.

Harvey's Austr. alg., No. 231 was examined in the herbarium in Paris, and I have also seen some specimens of the same number as above in several herbaria. The specimen in Paris is about 4.5 cm. long, branches and branchlets are not much thinner than the basal part of the frond, epiphytic on some corallinaceous algae. The branches are almost distichous, branches and branchlets are strongly patent, color is dark. In all specimens, surface cells are smooth, not projecting even at the top of the branchlets, strongly elongated radially and arranged evidently like palisade cells in the cross-section of

branchlets. There are no lenticular thickenings in the walls of the medullary cells.

In the mature stage, the frond of this species shows a slightly different appearance from that in the young stage, showing some resemblance to *L. botryoides* (Turner) Gaill., as was already noticed by J. Agardh. The difference of the anatomical characters, however, helps to separate them very easily.



E. *L. cruciata* Harv. Harvey's Austr. Alg. No. 231. × ca. 330.
A cross-section of a branchlet.

Section Forsterianae

Frond cylindrical or slightly compressed; the surface cells neither elongated radially, nor arranged like palisade cells in the cross-section of branchlets; there are many lenticular thickenings in the walls of the medullary cells.

The species belonging to the present section have always a considerable number of the lenticular thickenings in the walls of the medullary cells, though the number varies according to the different species, and according to the different individual, as well as to the different parts of one individual. Otherwise they are very similar to the species of the section *Cartilagineae*.

Laurencia pannosa Zanardini

Phyc. ind. pugil., p. 11, pl. 6, fig. *b*, 1, 2; Weber-van Bosse, Liste des alg. du Siboga, vol. 3, p. 344.

Type locality.—Sarawak.

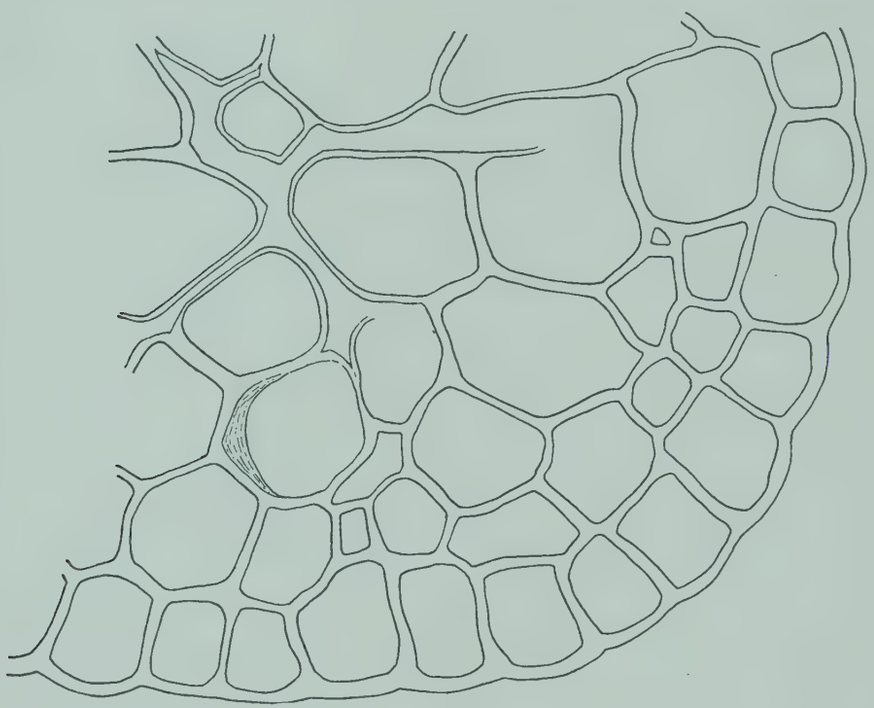
I have not been able to examine any of Zanardini's specimens of this species, but in the herbarium of Dr. Weber-van Bosse I have

studied the specimen from the Malay Archipelago named by her as *L. pannosa* Zan. In this specimen the surface cells are clearly projecting in the surface view, neither elongated radially nor arranged like palisade cells in the cross-section of branchlets; there are some lenticular thickenings in the walls of the medullary cells.

Laurencia mariannensis sp. nov.

Plate 5, figure *b*; figures F, G

Fronde laxe intricata, massam laxem humilem formanti, ca. 5 cm. alta, gracili, paniculatim ramosa; ramis ultimis cylindraceis vel clavatis, tetrasporangiiferis longe cylindraceis; cellulis superficialibus



F. *L. mariannensis,* sp. nov. The type specimen. × ca. 330. A cross-section of a branchlet.

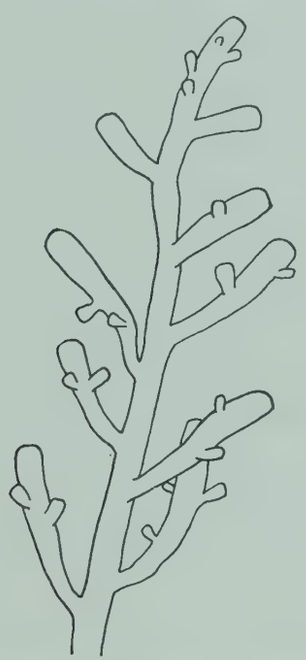
magnis, ad partem superiorem mammaeformiter projicientibus; cellulis superficialibus ad axem principalem longitudinaliter elongatis, 130–145μ longis, in sectione transversa rotundatis vel pauce radiatim elongatis; parte incrassata lenticulata ad parietes cellularum medullarum adeunte; cystocarpiis et antheridiis ignotis; colore flavescenti-rubro, substantia molli.

Habitat.—Saipan, Marianna Islands.

Frond loosely tufted, forming a loose mass, low, about 5 cm. high, slender, paniculately branched, ultimate branchlets cylindrical or clavate, tetraspore-bearing branchlets long cylindrical; cells large, those in apical parts of the frond mammaeform and projecting, surface cells large, often as large as medullary cells, round or slightly elongated radially in the cross-section, elongated longitudinally in the

surface view, about 130–145μ long in the main axis; there are lenticular thickenings in the walls of the medullary cells. Antheridia and cystocarps unknown.

The present species shows a very close relation to *L. pannosa* Zanard., judging from the specimens determined by Weber-van Bosse, although I have never studied any of Zanardini's specimens. According to the figures given by Zanardini, however, his species shows a cushion-like entanglement at the base, while in the present species this is not the case, and the Malayan specimens of Weber-van Bosse are much more slender than the present species.



G. *L. mariannensis*, sp. nov. A branch. × 6.

Laurencia pygmaea Weber-van Bosse

Mar. alg. of Sealark exped., Trans. Linn. Soc. bot., vol. 8, p. 122; Liste des alg. du Siboga, vol. 3, p. 344; De Toni, *l.c.*, vol. 6, p. 372.

Type locality.—The Chagos Archipelago.

At Eerbeek I have examined the type specimen of the present species. In that specimen, the surface cells are neither elongated radially, nor arranged like palisade cells in the cross-section of branches, not projecting in the surface view; there are several lenticular thickenings in the walls of the medullary cells.

The present species is related very closely to *L. pannosa* Zanard. as well as *L. mariannensis* Yam., but can be distinguished easily by the surface cells not projecting in the surface view. In branching it comes nearer to *L. pannosa* Zanard. than to *L. mariannensis* Yam.

Although I have distinguished these three species from one another I am not without doubt whether the specimens from three different places may not be merely different forms of the same species, which must be called *L. pannosa* Zanard. But because I have not seen any intermediate forms among them, I have listed them here as three different species.

Laurencia nidifica J. Agardh

Spec. alg., vol. 2, p. 749; Epicr. p. 649; De Toni, *l.c.*, p. 785.

Type locality.—The Hawaiian Islands.

In the Agardhian herbarium there are some specimens from the Hawaiian Islands. On the mounting paper of Nos. 36626 and 36628 there is a remark, "Woahoo Island, Sandw. Wilhne in Hb. Binder." No. 36627 is also from "Woahoo Island, Sandw. Wilhne" but there is no "in Hb. Binder" as in the preceding numbers. Numbers 36626 and 36627, however, bear the same number in pencil, "349," so most probably these three specimens are of one and the same origin, though their outer habits differ considerably from each other: Nos. 36627 and 36628 are rather similar, being slender and weak and having entangled bases, while No. 36626 is robust and provided with many short branchlets and is quite erect, recalling some small form of *L. papillosa* Grev. On the other hand, in the herbarium of the Royal Botanic Gardens, Kew, there is also a specimen sent by J. G. Agardh. This is quite like No. 36626 at Lund in habit, and also has the same number written in pencil as J. Agardh's specimen. I have examined the anatomical characters of this specimen at Kew through the kind permission of Dr. A. D. Cotton. The surface cells in this specimen are elongated radially and arranged like palisade cells in the cross-section of branchlets; there are no lenticular thickenings in the walls of the medullary cells.

On the other hand, in No. 36628 the surface cells are not arranged like palisade cells in the cross-section and there are some lenticular thickenings in the walls of the medullary cells.

As is clear from the above description, J. G. Agardh's specimens of *L. nidifica* are not uniform, and judging from the description given by the author we must take No. 36628 as the type of this species, and this species takes its systematic position among the *pannosa-pygmaea-mariannensis* group, or rather near *L. venusta* Yam. from Japan.

Laurencia venusta sp. nov.

Plate 6, figure *a*; figure H

Fronde parva ca 4 cm. alta caespitosa, ad basin laxe intricata, irregulariter pinnata, ramificatione non densa, ramis interdum curvatis, ramulis oppositis vel saepe verticillatis, ramulis ultimis breve clavatis, interdum secundatis, praecipue in ramulis curvatis; stichidiis compositis enormiter cymosis vel simplicibus; cellulis superficialibus forma inaequalibus, in sectione transversa pauce radiatim elongatis, simili modo ut cellulis valliformibus non dispositis, parietibus cellularum medullarum partem incrassatam lenticulatam ostendentibus; colore fusco-purpurea; cystocarpiis et antheridiis ignotis.



H. *L. venusta* sp. nov. A branch. × ca. 5.

Habitat.—Koshiki-jima, Prov. Satsuma; Goto, Prov. Hizen, Japan.

Frond small, about 4 cm. high, caespitose, loosely intricate at the base, irregularly pinnately branched, branching not dense, branches sometimes curved, branchlets opposite or often verticillate; ultimate branchlets shortly clavate, sometimes arranged secundly, especially on the curved branchlets; stichidial branchlets compound, irregularly cymose, or simple; epidermal cells irregular in shape, slightly elongated radially in the cross-section; lenticular thickenings abundant in the walls of the medullary cells. Color dark red. Cystocarps and antheridia unknown.

The specimens of this species were first collected by Yendo (in Goto), who identified them with *L. perforata* Mont. I have examined his specimens as well as Okamura's specimens from Koshiki-jima. These two collections appear to be slightly different from one another; Yendo's specimens being more intricate, showing more branches curved, and provided with secund branchlets and being darker in color. But these differences seem to me to be nothing but divergences caused by differences of outer conditions.

Laurencia radicans Kützing

Spec. alg., p. 853; Tab. phyc., vol. 15, pl. 50; De Toni, *l.c.*, p. 799.
Chondria radicans Kützing, Phyc. gen., p. 436.

Type locality.—Istria.

In the herbarium of Kützing at Eerbeek, there is the type specimen of the present species. In the walls of the medullary cells there are several lenticular thickenings; the surface cells are nearly quadrate in the cross-section of branchlets and their arrangement can not be called palisade-like; in the surface view they are not projecting. In external appearance this species bears some resemblance to *L. perforata* Mont. from the Canary Islands, but judging from the different anatomical structure it must be separated from Montagne's species.

Laurencia microcladia Kützing

Tab. phyc., vol. 15, p. 22, pl. 60, figs. *b*, *c*; Howe, in Britton and Millspaugh's Bahama Flora, p. 565.

Type locality.—West Indies.

I have examined the type specimen of Kützing, which was figured by him in Tabulae phycologicae, at Eerbeek, and have come to the same conclusion as Howe, who considers it an independent species as Kützing did, having found many lenticular thickenings in the walls of the medullary cells. Even in the small branchlets of the type specimen they are present in great numbers, and this species is to be separated from *L. obtusa* Lamx. very easily.

On the other hand, in the above cited work and also in the Flora Bermuda, Howe placed *L. glomerata* Suhr. in the synonymy of the present species. I have examined in the Agardhian herbarium a specimen under *L. glomerata* Suhr. (No. 36686 at Lund) which came from "La Guaryra-Peto Cabello ded. Binder" and found that this specimen belongs to the group of *L. obtusa* Lamx., and since I have not found

any lenticular thickenings in the walls of the medullary cells, I hesitate to follow Howe in considering *L. glomerata* Suhr. as a synonym of *L. microcladia* Kg., though I am not certain about the exact nature of *L. glomerata* Suhr.

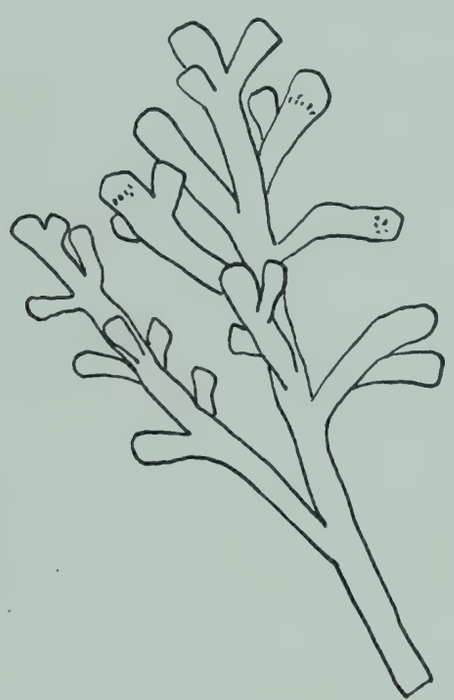
Laurencia indica Hauck

Plate 6, figure *b*; figure I

Über einige von Hildebrandt im Rot. Meere u. Ind. Ozean gesam. Alg. Hedwigia, vol. 27, p. 90; De Toni, *l.c.*, vol. 4, p. 794.

Type locality.—Mombasa, Zanzibar.

The type of *L. indica* Hck., preserved in the herbarium of the Botanical Museum in Berlin-Dahlem, consists of two specimens.



I. *L. indica* Hauck. A branch. × ca. 5.

They are about 5–6 cm. high, dark red, ramified very densely. On the other hand, four specimens from the same locality as that of the above specimens are preserved in the Thuret herbarium in Paris. They were collected by Hildebrandt and are to be found in the cover of *L. rigidula* Grunow. In these plants in Paris the surface cells do not show any arrangement like palisade cells in the cross-section of branchlets, and in the surface view they are not projecting; in the walls of the medullary cells of branches there is a considerable number of the lenticular thickenings.

In the same cover as above, there are two specimens sent from Grunow under the name of *L.* (*obtusa* var.?) *rigidula* Grun. which

were collected by Dr. Graeffe at Upolu, the Samoan Archipelago; they are very much like Hauck's specimens in habit, but they have no lenticular thickenings in the walls of the medullary cells and seem to belong to *L. obtusa* Lamx. In the herbarium of the Natural History Museum in Vienna, I have seen Grunow's specimens of his variety which are the same as the specimens in Paris, above mentioned.

Laurencia Okamurai sp. nov.

Plate 7; figures J, K

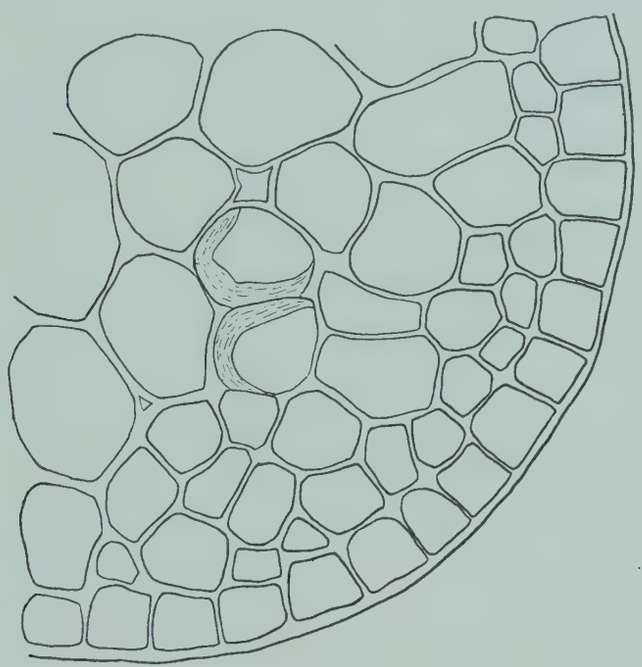
Radice fibrosa; fronde cartilaginea, 20 cm. alta et ultra, tereti, 1–2 mm. crassa, repetite pinnatim ramosa, caule principali percurrente quoquoversum ramosa, lineamentum paniculatum formanti; ramis patentibus, oppositis vel alternis vel subverticillatis; ramulis ultimis cylindraceis vel clavatis, apice truncatis vel rotundatis, simplicibus vel saepe in elongatis infra apices iterum ramosis; tetrasporangiis in ramulis ultimis conformibus situatis; cellulis superficialibus in sectione tranversa non radiatim elongatis, parietibus cellularum medullarum partem incrassatam lenticulatam abundanter ostendentibus; colore purpureo sed saepe flavescenti vel livido; cystocarpiis et antheridiis ignotis.

Habitat.—Bō, Prov. Satsuma; Kuchinotsu, Prov. Hizen; Tarematsu, Prov. Bungo; Shizukisan, Prov. Nagato; Sato, Prov. Kii; Deba-jima, Prov. Awa, Japan; Amoy, China.

Root fibrous; frond cartilaginous, 20 cm. long or more, cylindrical, 1–2 mm. thick at the base, repeatedly pinnately branched, main axis percurrent with paniculate outline; branches patent, opposite, alternate or subverticillate, ultimate branchlets cylindrical or clavate, truncate or rounded at apices, simple or longer ones sometimes again branched beneath apices; tetrasporangia on the ultimate branchlets of about the same shape as the sterile ones; cystocarps and antheridia unknown; surface cells not elongated radially in the cross-section of branchlets; lenticular thickenings abundant in the walls of the medullary cells. Color purple, but often fading to yellowish or blueish.

The present species appears to be distributed very commonly in the southern parts of Japan and previously has been referred by the phycologists to *L. obtusa* Lamx., whose type locality is in the southern part of England. The specimen which was described and figured by Okamura as *L. obtusa* Lamx. in his Icones appears to be, most probably, the present species, and Yendo named his specimens as varieties of *L. obtusa* Lamx. in his herbarium which now belongs to the Tokyo Imperial University. He named his specimens from Hizen Province as *L. obtusa* Lamx. var. *rigidula* f. *simplex* Grunow as well as f. *corymbosa* Grunow. Having examined the anatomical structure of

Yendo's specimens as well as of my own, also collected in the southern parts of Japan, I found many lenticular thickenings in the walls of the medullary cells of branches as well as branchlets. As pointed out by Howe, *L. obtusa* Lamx. has no lenticular thickenings in the walls of the medullary cells, so there is an important decisive difference between the preceding plant and Lamouroux's species. This is the principal reason for having given a new name to the present specimens, though there is some likeness between the Japanese plant and the Atlantic specimens, especially in the outer appearance.



J



K

J. *L. Okamurai,* sp. nov. The type specimen. × ca. 330. A cross-section of a branchlet.

K. *L. Okamurai* sp. nov. A branch. ×ca. 2.

Through the kindness of Professor N. L. Gardner, I have been able to examine some specimens of *Laurencia* from Amoy, China, which had been collected by Mr. H. H. Chung and sent to the University of California. Among them I have found some specimens which are to be referred to the present species, though the ultimate branchlets in these specimens are a little longer than those from Japan.

L. Okamurai is related very closely to *L. obtusiuscula* Set. et Gard. from Lower California, both species having many lenticular thickenings in the walls of the medullary cells even near the end of the ultimate branchlets, but they can be separated, one from the other, by the difference of branching.

Laurencia obtusiuscula Setchell et Gardner

Exped. of Calif. Acad. of Sci. to Gulf of Calif. Mar. Alg., Proc. Calif. Acad. Sci., vol. 4, p. 760, pl. 23, fig. 17.

Type locality.—Eureka, Lower California.

In the specimen of the type collection of this species, preserved in the herbarium of the University of California, the surface cells are neither elongated nor arranged like palisade cells in the cross-section of branchlets; there are many lenticular thickenings in the walls of the medullary cells.

The present species shows some resemblance to *L. indica* Hck., but can be easily distinguished by its great size and much shorter branchlets. The close relation to *L. Okamurai* Yam. has already been mentioned.

Laurencia Johnstonii Setchell et Gardner

L.c., p. 764, pls. 52*a*, 53.

Type locality.—Gulf of California.

I have examined one of the cotype specimens of the present species in Berkeley and found a considerable number of the lenticular thickenings in the walls of the medullary cells. The surface cells are not projecting in the surface view, neither elongated radially, nor arranged like palisade cells in the cross-section of branches.

Laurencia virgata J. Agardh

Plate 8, figures *a*, *b*

Spec. alg., vol. 2, p. 752; Epicr., p. 653; De Toni, *l.c.*, p. 793.
Laurencia versicolor Lamouroux, Ess. sur. gen. de fam. des thalas., p. 43 (non *Fucus versicolor* Vahl.).
Laurencia ericoides Kützing, Tab. phyc., vol. 15, p. 26, pl. 73, figs. *d-f*.

Type locality.—Cape of Good Hope.

In the Agardhian herbarium only Nos. 36978 and 36979 are from "Cap. b. Spei ex mus. Paris" and "Cap. b. Spei ex mus. Paris ded. Brongniart." In the herbarium of the Museum in Paris there are several specimens from the same locality as the Agardh specimens mentioned above and appear to be like them in habit. In these specimens there is a good number of the lenticular thickenings in the walls of the medullary cells in the branchlets. The surface cells are neither elongated radially nor arranged like palisade cells in the cross-section of branchlets; they are not projecting in the surface view.

Some specimens distributed by J. Agardh under the name of the present species in Alg. Müllerianae (west coast of New Zealand), have been examined in the herbarium of Thuret in Paris. They have the same characteristics as the Cape specimens in habit as well as anatomical structure. There are many lenticular thickenings in the walls of the medullary cells in the branchlets. *L. ericoides* Kg. was described from the Cape of Good Hope; having examined the type specimen, I consider it the same as the present species.

In the "Essai," Lamouroux mentioned the name of *Fucus versicolor* Vahl. among *Laurencia,* which was considered by J. Agardh as a synonym of *L. virgata* J. Ag., with a question mark (Spec. alg., vol. 2, p. 752). I have studied Lamouroux's specimens at Caen through the kindness of Professor R. Viguier, and found that his specimens are mostly the same as *L. virgata* J. Ag. On the other hand I was able to consult the original description of Vahl's *Fucus versicolor* and also to examine a fragment of this species through the kindness of Dr. F. Börgesen and have come to the conclusion that Lamouroux's *L. versicolor* is quite different from *Fucus versicolor* Vahl., which comes very near *L. obtusa* Lamx.

In many herbaria in Europe as well as in America we find some specimens from California under the name of the present species, but most of them appear to be *L. subopposita* Setch.

Laurencia nipponica sp. nov.

Plate 9

Fronde 27 cm. alta, teretiuscula, 1–2 mm. crassa cartilaginea, axi principali invicem percurrenti; ramulis paucis, sparsis papillaeformibus insitis et pinnatim nonnihil distiche ramosis; ramis brevibus inferiore 4–4.5 cm. longis, patentissimis, paniculatis; ramulis quoquoversum egredientibus, oppositis vel alternis vel subverticillatis; ramulis ultimis tetrasporangiiferis cylindraceo-clavatis, verrucosis, ad apices rotundatis, simplicibus vel divisis, praecipue ad ramulos superiorem saepe cymose fasciculatis; papillis ad axem principalem simplicibus vel corymbose compositis, saepe tetrasporangia foventibus; cellulis superficialibus rotundatis vel ellipsoideis, parietibus crassis ornatis, magnitudine inconstantibus, ad axem principalem ca. 60μ longis; in sectione transversa radiatim pauce elongatis, ca. 58–72μ longis, 39–52μ latis; partem incrassatam lenticulatam ad parietem cellularum medullarum ostendenti; cystocarpiis et antheridiis ignotis.

Habitat.—Japan: Oura, Prov. Nagato; Prov. Inaba; Noo, Prov. Echigo. China: Chifu.

Frond 27 cm. high, a little compressed, 1–2 mm. thick, cartilaginous, principal axis clearly percurrent, provided with scattered

papillae, pinnately branched, branchlets not distichous, opposite, alternate or verticillate on the branches; ultimate branchlets bearing tetrasporangia cylindrico-clavate, simple or divided, sometimes cymosely fasciculated, especially on the branches of the upper part of the frond, rounded at apices, verrucose; papillae on the principal axis simple or corymbose and producing tetrasporangia; surface cells round to ellipsoid in the surface view, with thick wall, variable in size, reaching about 60μ long in the principal axis, in the cross-section slightly elongated radially, about 58–72μ long, 39–52μ wide; lenticular thickenings present in the walls of the medullary cells. Cystocarps and antheridia unknown.

The present species is very peculiar in ramification, the definitely percurrent long principal axis being provided with rather short branches. The color is often yellow in the fertile condition.

In some specimens from Chifu, China, the branches in the lower part of the frond grow very long, giving the whole frond a pyramidal outline, and the principal axis is provided with numerous papillose branchlets, just as in the specimens from the Japanese coast. The stichidial branchlets are more simple than those of the latter, and the color is darker in the former. In spite of these differences, however, all the specimens show fairly good coincidence with those from Japan in anatomical structure, i.e., the presence of the lenticular thickenings in the walls of the medullary cells, the surface cells which are neither elongated radially nor arranged palisade-like in the cross-section of branchlets.

Laurencia Masonii Setchell et Gardner[2] var. **orientalis** var. nov.

Plate 10

Axibus principalibus ramulis minoribus in partibus superioribus intersparsis; ramis ultimis ad basin constrictis vel non constrictis, partibus incrassatis lenticulatis cellularum medullarum tenuioribus, numero multo paucioribus quam in typo.

Habitat.—Rishiri-tō, Hokkaido; Nemuro, Hokkaido, Japan.

In ramification, the plants of this variety are very close to the species, the main axes are sparsely provided with short branchlets in the upper parts; the ultimate branchlets are sometimes constricted at the base and sometimes not, but are more complicated than are those is the species; the thickenings in the walls of the medullary cells are thinner and much fewer in number than those of the type specimens.

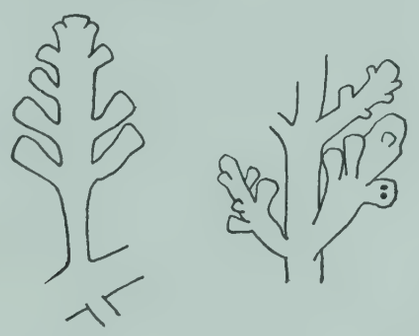
[2] Species from Clarion Island described in Proc. Calif. Acad. Sci., ser. 4, vol. 19, p. 155, 1931 (type station, Guadalupe Island, off Lower California).

The upper part of the main branches of the present specimens has some papillate branchlets which are entirely absent in *L. Masonii* Setch. et Gard., but the most important difference between the variety and the type of the species is the number and the shape of the lenticular thickenings in the walls of the medullary cells. I have compared a specimen of Setchell and Gardner in Berkeley: the lenticular thickenings in this specimen are very abundant even up to the tops of the branchlets, and their shape is very distinctive, being much thickened. In this point, my specimens from Hokkaido are sufficiently different to be separated from the species.

Laurencia japonica sp. nov.

Plate 11, figures *a*, *b*; figure L

Fronde 8 cm. alta, leviter compressa, bi- tripinnatim ramosa; ramis fere distichis, patentissimis, oppositis aut alternis, primo regularibus deinde ramulis brevibus dense obtectis; ramulis ultimis breve clavatis ad apices truncatis vel rotundatis; tetrasporangiis ad ramulos ultimos paniculatim compositos ramos densius obtectos gerentibus; cellulis superficialibus in sectione transversa tangentialiter pauce elongatis vel rotundatis; parietibus cellularum medullarum partem incrassatam lenticulatam ostendentibus; colore roseo-livido, substantia rigidiuscula; cystocarpiis et antheridiis ignotis.



L. *L. japonica* sp. nov. × ca. 4.

Habitat.—Amatsu and Emi, Prov. Boshu, Japan.

Frond 8 cm. high, slightly compressed, bi-tripinnately branched; branches nearly dichotomous, mostly open, opposite or alternate, becoming shorter upwards and forming, as a whole, a pyramidal outline; ultimate branchlets shortly clavate, truncate or rounded at apices; tetrasporangia produced on the ultimate branchlets which are paniculately compounded, and densely cover the branches in age; lenticular thickenings in the walls of the medullary cells present; the surface cells are slightly elongated tangentially or rounded, not arranged like palisade cells in the cross-section of branchlets; cystocarps and antheridia unknown.

The external appearance in the sterile condition of this species is quite different from that in the matured condition, being regularly pinnately branched, while the frond becomes much coarser and more irregular, and the smaller branches decompounded when matured.

The present species has some resemblance to *L. papillosa* Grev. in the external aspect, especially in age; it is distinguishable, however, from the latter species by the ramification and presence of the lenticular thickenings in the walls of the medullary cells and also the different shape and arrangement of the surface cells.

Laurencia coronopus J. Agardh

Plate 12, figure *a*

Spec. alg., vol. 2, p. 761; Epicr., p. 655; De Toni, *l.c.*, p. 796.

Type locality.—Taurid, Black Sea.

In the Agardhian herbarium, specimens Nos. 37080–37082 are mounted on one sheet, having in J. Agardh's handwriting the remark: "e littore Taurid in Hb. Ag. *Laurencia coronopus* J. Ag." and since they are in the best condition, they are most probably the type of the present species, although there are also some specimens in poorer condition in the same specific cover. Number 37080 is *ca.* 12.5 cm. high, caespitose, irregularly pinnato-paniculately branched, the ultimate branchlets are rather thick, inflated towards above, color dark. The surface cells are not projecting in the surface view, rather variable in shape in the cross-section of branchlets, being sometimes nearly square, sometimes slightly elongated radially or tangentially, but never arranged like palisade cells. The lenticular thickenings in the walls of the medullary cells are present in the branches, but not in the small branchlets.

Laurencia gracilis Hooker et Harvey

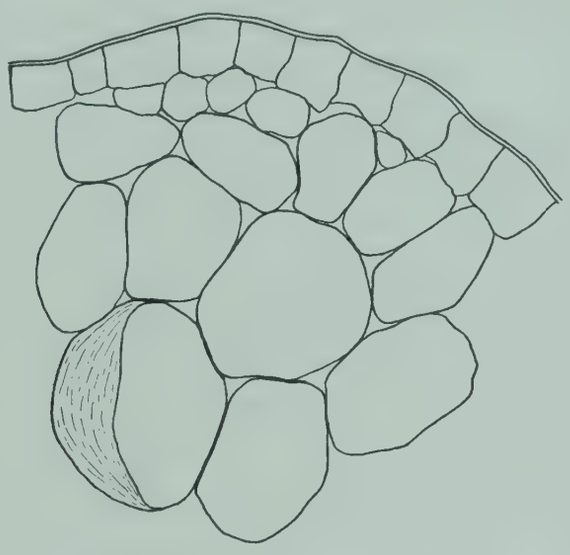
Plate 12, figure *b*; figure M

Harvey, Ner. austr., p. 84; J. Agardh, Spec. alg., vol. 2, p. 746; Epicr., p. 646; De Toni, *l.c.*, p. 780.

Type locality.—New Zealand.

In the herbarium of Hooker at Kew, there are three sheets of specimens under the name of this species which contain several specimens collected by Colenso in New Zealand (Colenso, No. 650), so they are undoubtedly the original specimens. In these specimens the frond is up to about 24 cm. high, slender, divided into some branches, showing no special main branch; branches are provided with sub-

pinnato-paniculate secondary branches, secondary branches patent sending again short branchlets, which are patent, often being inserted rectangularly to branches, inflated at the top. Color dark brown when dried, adhering to the paper imperfectly. The surface cells are usually elongated tangentially, not arranged like palisade cells in the cross-section of branchlets; not projecting in the surface view; the medullary cells have many clear lenticular thickenings in their walls, often even in the ultimate branchlets. In the Harvey herbarium at Dublin there are also several specimens which are of the same origin as Hooker's specimens, and both are exactly the same in every respect.



M. *L. gracilis* H. & H. Cotype specimen. × ca. 330.

In the present species the slenderness and dark color of the frond and the inflated branchlets are so peculiar that we may distinguish it very easily from other species.

J. G. Agardh considered that the present species was very nearly related to *L. Forsteri* Grev., but we must keep in mind that the specimen he obtained from Harvey or Hooker was a rather poor one, comparing it with several good specimens preserved now in the herbaria at Kew and Dublin.

Laurencia Forsteri (Mertens) Greville

Plate 13, figure *a*

Alg. brit. synop., p. lii; Harvey, Ner austr., p. 85; Kützing, Spec. alg., p. 854; Tab. phyc., vol. 15, pl. 46, figs. *c*, *d*, pl. 47, pl. 48; J. Agardh, Spec. alg., vol. 2, p. 744; Epicr., p. 645; De Toni, *l.c.*, p. 779.

Fucus Forsteri Mertens, in Turner's Hist. Fuc., pl. 77.

Chondria Forsteri C. Agardh, Spec. alg., vol. 1, p. 343.

Type locality.—Australia.

In the herbarium of the Royal Botanic Gardens, Kew, there is the specimen of Turner which was collected by Menzies and drawn by Turner in his *Fuci.* In this specimen the surface cells are neither elongated radially nor arranged like palisade cells in the cross-section of branchlets, not projecting in the surface view; there are lenticular thickenings in the walls of the medullary cells of the branches.

In branching and texture, the present species appears to be exceedingly variable, and these extreme forms were described as an independent species by the earlier phycologists. *L. affinis* Sonder appears to me to be nothing but an old hard form of the present species. So I put it under the formal rank of *L. Fosteri* Grev. *L. heteroclada* Harv. comes very near the present species especially form *affinis,* but can be distinguished from it by its special arrangement of the stichidial branchlets as well as by the absence of the lenticular thickenings in the walls of the medullary cells.

Forma **affinis** comb. nov.

Laurencia affinis Sonder

Alg. Preiss, Bot. Zeitung, p. 55, 1845; Harvey, Ner. austr., p. 84; Kützing, Tab. phyc., vol. 15, pl. 45, figs. *c, d*; J. Agardh, Spec. alg., vol. 2, p. 744; Epicr., p. 646; De Toni, *l.c.*, p. 780.

Type locality.—Australia.

In this form, the frond is rather rigid and much branched. Several specimens distributed from the herbarium of Binder under the name of *L. affinis* Sond. are preserved in different herbaria. They are subfuscous in color, very hard in texture, and in the walls of the medullary cells of the branches there are several lenticular thickenings.

Sonder distinguished *L. affinis* from *L. Forsteri* Grev. by subfuscous color, condensed ramification and irregularly divided branchlets which are attenuated at the base, but as had been already indicated by J. Agardh, such characteristics are very unreliable for distinguishing these species one from the other.

Laurencia scoparia J. Agardh

Plate 13, figure *b*; figure N

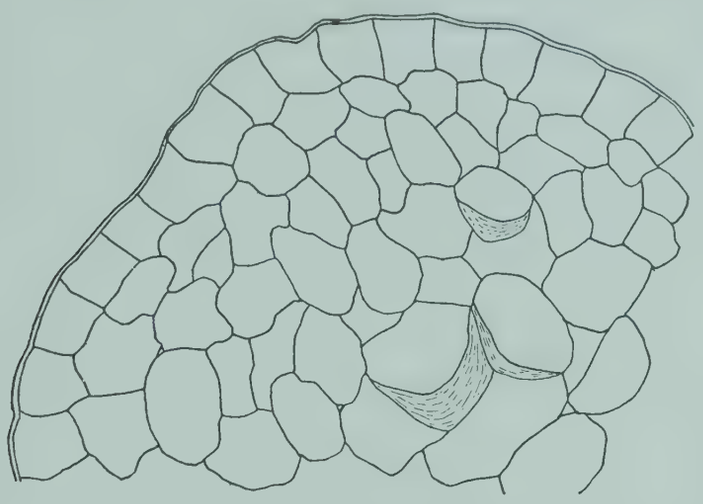
Spec. alg., vol. 2, p. 746; Epicr., p. 648; De Toni, *l.c.*, p. 784.

Type locality.—La Guayra.

In Agardh's herbarium at Lund, there are four numbers of specimens in the cover of this species: Nos. 36610–36613. Number 36610 is

from "La Guayra & Puerto Cabell ded, Binder" and consists of a large specimen which is about 8 cm. high, and two small specimens; they are most probably the type of the present species. I have examined the large specimen. The surface cells are nearly square or slightly elongated radially or sometimes slightly elongated tangentially in the cross-section of the upper part of branches, and are not arranged like palisade cells. In the walls of the medullary cells there are many lenticular thickenings.

The present species seems to come very near *L. Forsteri* Grev.



N. *L. scoparia* J. Ag. (No. 36613 at Lund). × ca. 330.
A cross-section of a branchlet.

Section Cartilagineae

Frond cylindrical or slightly compressed, the surface cells neither elongated radially, nor disposed like palisade cells in the cross-section of branchlets; lenticular thickenings in the walls of the medullary cells are absent or, if present, very few in number.

The present section includes many species different in habit; very strong plants like *L. tasmanica* Harv., *L. tropica* Yam., etc., and also very weak forms like *L. chondrioides* Börg., and in the arrangement of the stichidial branchlets they are not uniform, some showing compound ones like *L. heteroclada* Harv., etc., while the others have simple stichidial branchlets like *L. glandulifera* Kg., etc. The latter characteristic is not always constant, for even in one species, viz., *L. obtusa* Lamx., they are usually simple, while very often the compound ones are found in a form which was named by Bory *L. pyramidalis*.

In most species grouped here the lenticular thickenings are wanting, but in a few species, viz., *L. corymbosa* J. Agardh, they are found sometimes.

Laurencia nana Howe

Britton and Millspaugh, Bahama Flora, p. 566.

Type locality.—Bahama Islands.

Number 207519 of the herbarium of the University of California, distributed by Howe as No. 5393 of the herbarium of the New York Botanical Garden, I have studied in Berkeley. In habit it is very like the figure of *L. pannosa* Zanard. In the Bahaman specimen, however, the surface cells are not projecting in the surface view, neither elongated radially, nor arranged like palisade cells in the cross-section of branches. I have found no lenticular thickenings in the walls of the medullary cells.

In the herbaria at Eerbeek and at Berlin-Dahlem I have seen several specimens of Kützing, named by him as *L. nana* Kg., which belong to the section Palisadae; their frond is small, being about 2–3 cm. high and appear to come very near *L. papillosa* Grev. The name of this species, however, does not seem to have been published anywhere.

Laurencia claviformis Börgesen

Mar. alg. from Easter Isl., Ext. from Nat. hist. Juan Fernandez and Easter Islands (ed. by Dr. Skottsberg), p. 298, fig. 39.

Type locality.—Easter Island.

The type material of the present species is preserved on slides in the Botanical Museum at Copenhagen. The surface cells are not projecting in the surface view, neither elongated radially, nor arranged like palisade cells in the cross-section of branches. I have found no lenticular thickenings in any sections.

Laurencia brachyclados Pilger

Alg. Mildbr. Annob., p. 6, figs. 9, 10.

Type locality.—Annobon, Guinea.

The type specimens are in Berlin-Dahlem, where six specimens are mounted on one sheet. They were at first preserved in alcohol, hence are completely decolorized; branches fastigiate, being quite different from the branching in *L. perforata* Mont. to which the present species was referred by De Toni. But this amalgamation does not seem to me to be correct because of the difference in branching as well as in anatomical character. In Pilger's plant the surface cells are not projecting in the surface view, slightly elongated tangentially in the

cross-section of branches, and so are not disposed like palisade cells. So far as I have been able to determine, there are no lenticular thickenings in the walls of the medullary cells.

The present species is related very closely to *L. claviformis* Börg.

Laurencia chondrioides Börgesen

Mar. alg. of Dan. West Ind., vol. 2, p. 252; De Toni, *l.c.*, vol. 6, p. 370.

Type locality.—St. Jan, West Indies.

The type specimen of the present species is preserved in the herbarium of the Botanical Museum of Copenhagen. It seems to be a very delicate plant, growing always in deep water. In the superficial view the surface cells of the branchlets are slightly projecting near the top, which is suggested in figure 244 of Börgesen. There is no lenticular thickening in the walls of the medullary cells.

The present species comes very near *L. mariannensis* Yam. from the Pacific, having very delicate fronds and projecting surface cells, but in the latter species the surface cells are more strongly projecting and in the walls of the medullary cells there are considerable numbers of the lenticular thickenings; also the difference of branching assists in separating them one from the other.

Laurencia seticulosa (Forskaal) Greville

Alg. brit. synop., p. lii; Kützing, Spec. alg., p. 857; Tab. phyc., vol. 15, pl. 52; J. Agardh, Spec. alg., vol. 2, p. 758; Epicr., p. 652; De Toni, *l.c.*, vol. 4, p. 790.

Conferva seticulosa Forskaal, Flor. aeg. et arab., p. 188.

Type locality.—Red Sea.

In Agardh's herbarium No. 36833 was sent by Forskaal, probably representing a cotype specimen. The superficial cells are not projecting in the surface view, not elongated radially in the cross-section. The lenticular thickenings in the walls of the medullary cells are not present, at least in the small branches.

Laurencia capituliformis sp. nov.

Plate 14

Fronde 14 cm. alta, leviter compressa, ca. 1.5 mm. crassa, axe principali percurrente, non flexuosa, bi- tripinnatim fere distiche ramosa, pyramidatum lineamentum formanti; ramis alternis vel subopositis, longitudine sursum sensim diminuendibus, inferiore 10 cm., superiore 1–2 cm. longis, patentissimis, paniculatis; ramulis ultimis

tetrasporangiiferis brevibus, capitatissimis, plerumque tuberibus verrucaeformibus ornatis; cellulis superficialibus axis principalis longitudinaliter elongatis, ca. 100μ longis in sectione transversa leviter radiatim elongatis, nonnihil simili modo ut cellulis valliformibus dispositis, partem incrassatam lenticulatam ad parietes cellularum medullarum non ostendentibus; colore flavo-purpureo, substantia molli; cystocarpiis et antheridiis ignotis.

Habitat.—Oshima, Prov. Mutsu, Japan.

Frond about 14 cm. high, slightly compressed, about 1.5 mm. broad, principal axis percurrent, not flexuous, 2–3 times pinnately branched, nearly distichous, branches alternate or subopposite, their length diminishing upwards, so that the whole plant shows a pyramidal outline, widely spread, paniculate, about 10 cm. long in the lower part, about 1–2 cm. long in the upper part; ultimate branchlets bearing tetrasporangia short, strongly capitate, usually provided with wart-like protuberances; surface cells of the principal axis elongated longitudinally, reaching about 100μ in length in the surface view, slightly elongated radially in the cross-section, showing somewhat of a palisade-like arrangement; there are no lenticular thickenings in the walls of the medullary cells; cystocarps and antheridia unknown; color reddish yellow; texture rather soft, adhering well to paper on drying.

This new species seems to be closely related to *L. botryoides* (Turn.) Gaill., but is distinguishable from the latter by not having a flexuous frond and by the shape of the stichidia. On the other hand, *L. distichophylla* J. Ag. according to the description, appears to have some resemblance with the present species, but the shape of the stichidia is so different in the new species that we can easily distinguish them, one from the other.

Laurencia glandulifera Kützing

Spec. alg., p. 855; Tab. phyc., vol. 15, pl. 59, figs. *c*, *d*.

Chondria glandulifera Kützing, Phyc. germ., p. 329.
Laurencia paniculata J. Agardh (*pro parte*), Spec. alg., vol. 2, p. 755; Epicr., p. 651.
Chondria obtusa var. *paniculata* Agardh (*pro parte*), Spec. alg., p. 343.

Type locality.—Triest, Adriatic Sea.

Both C. Agardh and J. Agardh confused the present species with *L. paniculata* J. Ag., as I have mentioned under the latter species.

The present species usually has a very soft frond, much softer than that of *L. paniculata* J. Ag., and the surface cells are neither elongated radially, nor arranged like palisade cells in the cross-section of branchlets. From *L. obtusa* Lamx. the present species can be distinguished by its very short ultimate branchlets.

Some specimens which are common in the northern parts of Japan and have passed as *L. paniculata* J. Ag. among us, appear to me to be referable to the present species.

Laurencia Poitei (Lamouroux) Howe

Plate 15, figure *a*

Phyc. stud., vol. 2, p. 583 (Bull. Torr. Bot. Club, vol. 32); Britton and Millspaugh, Bahama Flora, p. 566; Börgesen, Mar. alg. of Dan. West Ind., vol. 2, p. 245; De Toni, *l.c.*, vol. 6, p. 373.

Fucus Poitei Lamouroux, Dissert. sur plus. espec. de Fucus, p. 63.

Laurencia Mexicana Kützing, Tab. phyc., vol. 15, p. 25, pl. 70, figs. *c, d.*

Laurencia tuberculosa J. Agardh, Spec. Alg., vol. 2, p. 760; Epicr., p. 657; De Toni, *l.c.*, vol. 4, p. 801.

Gracilaria Poitei J. Agardh, Spec. alg., vol. 2, p. 596; Epicr., p. 421.

Type locality.—Santo Domingo.

Howe studied the type specimen of *Fucus Poitei* Lamx., gave precise information about it and made the new combination, *L. Poitei* (Lamx.) Howe. I have also studied the type through the kindness of Professor Viguier at Caen. In this type specimen, the superficial cells are not projecting in the surface view, neither elongated radially, nor arranged like palisade cells in the cross-section of branchlets; there are no lenticular thickenings in the walls of the medullary cells.

On the other hand, I have seen the same characteristics in the type specimen of *L. mexicana* Kg. at Eerbeek as in the Lamouroux type specimen, and so there can be no doubt about the identity of Kützing's species with the present one. I have also seen the specimens of *L. tuberculosa* J. Ag. at Lund, which is to be united with the present species.

L. brasiliana Mart. is placed in the synonymy of *L. tuberculosa* J. Ag. in De Toni's Sylloge Algarum. The type specimen of von Martens is now preserved in the herbarium of the Botanical Museum of Berlin-Dahlem. It consists of two poor specimens which are very similar in habit, being 5–6 cm. high, without a clear percurrent principal axis and showing branches strongly patent. The surface cells are not projecting in the surface view, neither elongated nor arranged like palisade cells in the cross-section of branchlets.

This species seems to come very near *L. Poitei* (Lamx.) Howe, but the available specimens are not sufficient for proposing to unite it with *L. Poitei* (Lamx.) Howe.

var. **gemmifera**

Laurencia gemmifera Harvey, Ner. bor. amer., vol. 2, p. 73, pl. 18 *b*; Howe, in Britton and Millspaugh's Bahama Flora, p. 566.

Laurencia tuberculosa var. *gemmifera* J. Agardh, Epicr., p. 657; De Toni, *l.c.*, p. 802.

Laurencia Chauvini Bory pro part., Dict. class. d'hist. nat., vol. 9, p. 239.

Type locality.—Key West.

In Harvey's herbarium at Dublin, there are several specimens in the cover of the species *L. gemmifera* Harv., of which one was figured in Nereis Boreali-Americana, and came from Key West, so undoubtedly the type specimen. In this specimen as well as in others, the surface cells of branchlets are strongly projecting in the surface view, especially near the top, and often mucronate, as already noticed by Howe and other botanists. In the cross-section of branchlets, they are nearly square or very slightly elongated radially in shape, but are not arranged like palisade cells; in size, there is not much difference between them and the medullary cells; there are no lenticular thickenings in the walls of the medullary cells, at least in the branchlets. In the Thuret herbarium, as well as in the general herbarium in Paris, there are several specimens of Bory from Bahama named by him as *L. Chauvini* Bory. As had been already noticed by Howe, many of them represent *L. intricata* Lamx., while others are *L. gemmifera* Harv.

So far as I know, the present variety appears to be limited to the Atlantic side of America. Weber-van Bosse reported *L. gemmifera* Harv. from the Malay Archipelago in her Siboga List, vol. 3, p. 345. She was kind enough to allow me to examine her specimens at Eerbeek and having examined them, I have come to the conclusion that they belong to the *Palisadae,* being provided with the surface cells clearly disposed palisade-like in the cross-section of branchlets, and they are most probably to be referred to *L. paniculata* J. Ag.

Laurencia hybrida (De Candolle) Lenormand

Duby's Bot. gall., p. 951; Kützing, Spec. alg., p. 856; Tab. phyc., vol. 15, pl. 65, figs. *b, c*; J. Agardh, Spec. alg., vol. 2, p. 761; Epicr., p. 655; De Toni, *l.c.*, p. 796; Cotton, Clare Isl. survey, mar. alg., p. 136.

Fucus hybridus De Candolle, Flor. franc., vol. 2, p. 30.

Fucus pinnatifidus var. *angustus* Turner, Hist. Fuc., pl. 20, fig. *f*; Harvey, Phyc. brit., pl. 55.

Laurencia caespitosa Lamouroux, Ess. sur. gen. de fam. des thalas., p. 43; Harvey, *l.c.*, pl. 286.

Type locality.—Calvados, France.

The confusion about the synonymy of this species was elucidated by Cotton in his Clare Island Survey. In the spring of 1929 I observed many living specimens of this species at Sant-Serven, France. In this species, there are no lenticular thickenings in the walls of the medullary cells; the surface cells are usually elongated tangentially and are not disposed like palisade cells in the cross-section of branchlets; they are not projecting in the surface view.

Laurencia canarienses Mont. was described and figured by Kützing, based upon Montagne's specimen which had been considered by Montagne to be *L. caespitosa* Lamx. (= *L. hybrida* Lenorm.). At Eerbeek I have seen the type specimen of this species. It shows some resemblance to the type specimen of *Fucus perforatus* Bory in habit, but in shape and arrangement of surface cells it is very different from Bory's species, being neither elongated radially nor arranged like palisade cells in the cross-section of branchlets. In the herbarium of Montagne in Paris there are some seven specimens which seem to have been considered by Montagne as *L. canariensis* Mont. But these specimens are all in a rather poor condition and do not appear to be uniform.

Laurencia subopposita (J. Agardh) Setchell

Plate 15, figure *b*

Paras. Florid., Calif. Univ. pub. in bot., vol. 6, p. 9.
Chondriopsis subopposita J. Agardh, Anal. alg., p. 149.

Type locality.—Santa Barbara, California.

In the Agardhian herbarium at Lund Nos. 37629–37633 were collected by Mrs. Bingham at Santa Barbara, so undoubtedly represent the type. In these specimens the surface cells are nearly quadrate, not disposed like palisade cells in the cross-section of branchlets, not projecting in the surface view; there are no lenticular thickenings in the walls of the medullary cells, so far as I have examined.

As Setchell has pointed out, this species is confused with *L. virgata* J. Ag. in many herbaria. Phycotheca boreali-americana, No. 293 and No. 1495, and also No. 60 of Alg. exsic. amer. bor. of Farlow, Anderson and Eaton under the name of *L. virgata* J. Ag. appear to belong to the present species, though their ramification is slightly different from that of the type.

Laurencia obtusa (Hudson) Lamouroux

Plate 16, figures *a*, *b*, *c*; plate 17, figures *a*, *b*, *c*

Ess. sur gen. de fam. des thalas., p. 42; Greville, Alg. brit., p. 111; Harvey, Phyc. brit., pl. 148; Kützing, Spec. alg., p. 854; Tab. phyc., vol. 15, pl. 54, 55; J. Agardh, Spec. alg., vol. 2, p. 750; Epicr., p. 653; De Toni, *l.c.*, p. 791.

Fucus obtusus Hudson, Flora angl., p. 586; Turner, Hist. Fuc., pl. 21; Velley, Col. fig. of mar. plants.

Chondria obtusa C. Agardh, Spec. alg., vol. 1, p. 340.

Laurencia pyramidalis Bory, in Kützing's Spec. alg., p. 854.

Laurencia multiflora Kützing, Tab. phyc., vol. 15, p. 21, pl. 58, *a*, *b*.

Laurencia oophora Kützing, Tab. phyc., vol. 15, p. 20, pl. 57, figs. *a*, *b*.

?Laurencia cymosa Kützing, *l.c.*, p. 21, pl. 57, figs. *c*, *d*.

Type locality.—England.

This species varies strongly in the external appearance, but the frond is usually rather soft, not cartilaginous, cylindrical, and never shows the radially elongated surface cells in the cross-section of branchlets being arranged like palisade cells, and even in a well grown specimen there are no lenticular thickenings in the walls of the medullary cells. Falkenberg gave some figures of this species in his Rhodomelaceen des Golfes von Neapel, but one of them, having radially elongated surface cells in the longitudinal section, does not seem to me to belong to the present species. I wonder whether he might have confused the present species with *L. paniculata* J. Ag.?

In the herbarium of the Royal Botanic Gardens, Kew, there is an old specimen in the cover of *L. obtusa* var. *laxa* Ardiss., which is accompanied by a label with Harvey's remark reading: "This seems to be the original specimen on which Turner founded his *Fucus laxus* —a plant which has puzzled every one since! (it seems to be a var. of *L. obtusa*). To be kept!! W. H. H." And on the mounting paper, "no. 3. Cape of Good Hope. Mr. Brown. 1807." In this, Turner's type specimen, the frond is about 15 cm. long, slightly compressed, pinnately branched, branching very loose, reminding one of a form of *L. obtusa*. The surface cells are neither elongated radially, nor disposed like palisade cells in the cross-section of branchlets; there are no lenticular thickenings present in the walls of the medullary cells. In De Toni's Sylloge Algarum, Turner's *Fucus laxus* is placed in the synonymous position of *Chondria capensis* Harv., but this is evidently not correct, though I can not say much about this specimen. The specimens of Kützing under the same of *L. laxa* Grev. preserved in

Berlin-Dahlem, appear to come nearer to *L. obtusa* Lamx. than this Turner specimen does. Besides the typical form which is common in the Atlantic, I will mention the following varieties:

var. **divaricata**

Laurencia divaricata J. Agardh, Spec. alg., vol. 2, p. 754; Epicr., p. 649; De Toni, *l.c.*, p. 786.

Type locality.—Red Sea.

In the cover of *L. divaricata* J. Ag. in the Agardhian herbarium, there are eight sheets including specimens rather different in external appearance. The only Red Sea specimens are Nos. 36642–36644, and the other specimens are from Australia and Key West (No. 36643 has no remark concerning the locality, but probably of the same origin as the No. 36642). Among these specimens No. 36642, which was sent from Requien, is most probably the type, while on the mounting paper of No. 36644, there is a remark reading, "*Laurencia cyanosperma* Lamx. mer. rouge" (probably in Lamouroux's handwriting). The type specimen is about 9 cm. long, caespitose, paniculately branched, ultimate branchlets are short.

As to the anatomical characters, there are no lenticular thickenings in the walls of the medullary cells, at least near the end of the branches; the surface cells are not projecting in the surface view; in the cross-section of branchlets, they are nearly square or slightly elongated tangentially and are not arranged like palisade cells. In this cover Harvey's Australian algae Nos. 230B and 230C are also preserved.

var. **majuscula** Harvey

Phyc. austr. syn., No. 309*b*; Aust. alg., No. 236.

Type locality.—Western Australia.

In several herbaria I have examined Harvey's Australian algae No. 236 as well as Harvey's Ceylon algae No. 20 and Ferguson's Ceylon algae Nos. 159 and 334. They are all referable to the present variety, but they show fewer branches than the first mentioned specimen. Specimens of this variety were distributed by Harvey as No. 236 of the Australian algae and considered by J. Agardh and other phycologists to be the same as *L. dendroidea* J. Ag. whose type locality is Brazil. In this variety, the frond is usually beautifully red and the surface cells are slightly projecting in the surface view near the end of the branchlets.

This variety seems to be distributed widely in the warmer parts of the Atlantic, Pacific, and also Indian Ocean. I have examined some specimens to be referred to the present variety in the collection of Mr. K. G. Iyengar which was made at Dwarka, the northwestern coast of East India, and sent to Professor Setchell at the University of California for identification. In the southern parts of Japan it occurs very often, sometimes together with *L. Okamurai* Yam., but it is very easy to distinguish them, one from the other, by the characters of the surface cells and also by the lenticular thickenings in the branchlets.

In the herbarium of Kützing in Eerbeek, there is only one specimen of *L. Vieillardi* Kg. which was figured by Kützing in Tabulae phycologicae, vol. 15, pl. 45, so undoubtedly the type specimen. In this specimen, the frond is very thin, the surface cells are neither elongated radially, nor arranged like the palisade cells in the cross-section of branchlets; in the surface view they are not projecting at the end of the ultimate branchlets.

J. Agardh considered this species to be the same as *L. dendroidea* J. Ag., though with some doubt. For me this species seems to come most nearly to the present variety, but it is rather difficult to obtain the exact idea of the species from this single specimen.

var. **dendroidea**

Laurencia dendroidea J. Agardh, Spec. alg., vol. 2, p. 753; Epicr., p. 650; De Toni, *l.c.*, p. 787.

Type locality.—Brazil.

In the herbarium of J. Agardh there are six sheets and some unmounted specimens in the cover of *L. dendroidea* J. Ag. of which only No. 36696 came from "Brasilia Lund," and this has very different habit from other specimens, showing many slender branchlets. This specimen has no lenticular thickenings in the walls of the medullary cells, at least in the small branchlets; the surface cells are neither elongated radially, nor arranged like palisade cells in the cross-section of branchlets; in the surface view, they are not projecting.

At Lund in the cover mentioned above are included Harvey's Australian algae No. 236A and B, which I have already referred to the preceding variety. Okamura's Algae Exs. Jap. No. 20, distributed under the name of *L. dendroidea* J. Ag., is clearly not that species; as I have already mentioned under *L. intermedia* Yam. At any rate, *L. dendroidea* J. Ag., *L. obtusa* var. *majuscula* Harv., and *L. Vieillardi*

Kg. have been very much confused with one another in many herbaria. In this variety the frond has no surface cells projecting and the branches are finer than in other varieties. Most specimens named as *L. dendroidea* J. Ag. or *L. Vieillardi* Kg. by J. Agardh and many earlier phycologists appear to me to be different from the type specimen of *L. dendroidea* J. Ag., at least in variety; they mostly belong to the above variety, as has been mentioned.

var. **Snackeyi**

Laurencia paniculata J. Ag. f. *Snackeyi* Weber-van Bosse, Liste des alg. du Siboga, vol. 3, p. 342.

Type locality.—Samau Island, near Timor.

The present variety has very thick branches compared with other varieties; the surface cells are not projecting as in var. *majuscula* Harv. I have studied the type specimen of Weber-van Bosse at Eerbeek, and as it does not show any characteristics of *Palisadae* it seems to me to be more reasonable to consider it a variety of *L. obtusa* Lamx. than of *L. paniculata* J. Ag. In the Palao Island I also have met with the present variety myself.

var. **rigidula** Grunow

Alg. Fidschi, Tonga, u. Samoa Ins., p. 23.
Laurencia obtusa var. *squarrosa*, Grunow, *l.c.*, p. 23.

Type locality.—Upolu, Samoan Archipelago.

The present variety represents a small rigid form which is very common in the warmer parts of the Pacific. *L. obtusa* Lamx. var. *squarrosa* Grun. does not seem to me to be a different variety from var. *rigidula* Grun. I have seen the type specimens of these varieties in the herbarium of Natural History Museum in Vienna, and have examined the specimens determined by Grunow in the Thuret herbarium in Paris.

var. **intricata** comb. nov.

Laurencia intricata Lamouroux. Ess. sur gen. de fam. des thalas., p. 43, pl. 9, figs. 8, 9; J. Agardh, Spec. alg., vol. 2, p. 750; Epicr., p. 649; De Toni, *l.c.*, p. 786.

Chondria intricata Montagne. Hist. phys. polyt. et nat. de l'ile Cuba, Bot. Plant. cell., p. 41.

Laurencia implicata J. Agardh, Spec. alg., vol. 2, p. 745; Epicr., p. 646; Harvey, Ner. bor. amer., vol. 2, pl. 18, fig. *D;* De Toni, *l.c.*, p. 781; Börgesen, Mar. alg. Dan. West Ind., vol. 2, p. 251.

Type locality.—The Antilles.

In Lamouroux's herbarium in Caen, as well as in the general herbarium of the National Museum of Natural History in Paris, there are Lamouroux specimens from "Ameriq. septent." I have studied these specimens as well as Bory's specimens of *L. Chauvini* Bory in Paris. They do not seem to me to be different specifically from *L. obtusa* Lamx., as already suggested by Howe. As has also been reported by the same phycologist, Bory's specimens of *L. Chauvini* Bory include another different species, *L. Poitei* Howe var. *gemmifera.* At Lund I have seen some specimens of *L. implicata* J. Ag. which appear to be the same as Lamouroux' species.

J. G. Agardh doubted whether Harvey's *L. cervicornis* (Ner. bor. amer., pl. 18, fig. *C*) might be the same as *L. implicata* J. Ag., but Howe also has shown that *L. cervicornis* Harv. is a synonym of *L. corallopsis* Howe, which belongs to the *Palisadae.*

var. **densa** var. nov.

Fronde molli, 6–7 cm. alta, teretiuscula, gracili, ca. 1 mm. crassa, ramulis brevibus dense obtecta; ramulis enormiter quoquoversum egredientibus, brevibus; ramulis ultimis comparate longis cylindraceis, ad apices truncatis vel leve rotundatis, irregularibus, interdum alternis; tetrasporangiiferis conformibus; cellulis superficialibus forma irregularibus, in sectione transversa radiatim aut tangentialiter pauce elongatis vel rotundatis ca. 25μ latis; parte incrassata lenticulata ad parietem cellularum medullarum non adeunte; colore fusco-livido.

Habitat.—Daibanratsu, Formosa.

Frond soft, about 6–7 cm. high, slightly compressed, slender, about 1 mm. thick, covered densely with short branches; branches irregular, short; ultimate branchlets comparatively long, cylindrical, truncated or a little rounded at apices, arranged irregularly, sometimes alternate; stichidia exactly like the sterile branchlets in shape; cystocarps and antheridia unknown; surface cells irregular in shape, sometimes slightly elongated radially, sometimes tangentially or round in the cross-section, about 25μ diameter, no lenticular thickenings in the walls of the medullary cells.

Laurencia filiformis Montagne

Plate 18, figure *a*

Voy. au pole sud, p. 125; J. Agardh, Spec. alg., vol. 2, p. 745; Epicr., p. 644; De Toni, *l.c.*, p. 779.

Chondria filiformis C. Agardh, Spec. alg., vol. 1, p. 358.

Type locality.—Australia.

In the general herbarium of the National Museum of Natural History in Paris, there are two sheets of specimens of this species accompanied by a label which is in J. G. Agardh's handwriting, reading: "*Chondria filiformis* Ag. Syst. J. Agardh." They were collected by Leschenault in Australia, so there is no doubt about the fact that they are the specimens quoted by C. Agardh, and represent the type of *Chondria filiformis* C. Ag. The first sheet contains three good specimens, while on the other are mounted five specimens including small fragments. In the same cover, there is another specimen, cystocarpic, which was also collected by Leschenault in Australia but without J. Agardh's handwriting on the label. They all represent very weak plants, being much like Montagne's specimens which will be described below, but less branched. In the cross-section of branchlets, the surface cells are neither elongated radially, nor arranged like palisade cells, not projecting in the surface view; there are no lenticular thickenings in the walls of the medullary cells. On the other hand, Montagne gave two localities in his original description of *L. filiformis* Mont., "Hab. ad insulam Toud. d'Urville, ad terram Van Diemon cl. Dubouzet legerunt." In his herbarium in Paris both these specimens are preserved. In these specimens, the cell walls are rather thick, but I have found no lenticular thickenings in the frond; the surface cells are nearly quadrate or slightly elongated tangentially in the cross-section of branchlets.

The present species seems to come very closely to *L. Forsteri* Grev., so closely that at one time I was tempted to consider it a weak form of that species, but I have never found any lenticular thickenings in the walls of the medullary cells, even in the cystocarpic specimen of Leschenault, above mentioned.

Laurencia chilensis De Toni, Forti et Howe

Atti R. Instituto, Veneto, 79, p. 689; Nuova Notarisia, 32, p. 150, figs. 1–3; De Toni, *l.c.*, vol. 6, p. 369.

Type locality.—Chili.

I have not been able to examine any specimens of this species except a fragment in the herbarium of the New York Botanical Garden, but according to the description and figures in Nuova Notarisia the surface cells are slightly crenulate-mammillate or smooth in the surface view, neither elongated radially, nor arranged palisade-like in the cross-section; the walls of the medullary cells are not provided with any lenticular thickenings.

Laurencia clavata Sonder

Plant Muell., Linnea, vol. 25, p. 694; Schmitz, Engler u. Prantl's Nat. Pflanzenfam., p. 431; Falkenberg, Rhodomelac. des Golf. von Neapel, p. 251; Weber-van Bosse, Liste des alg. du Siboga, vol. 3, p. 346.

Chondria corynephora Harvey, Some acc. of mar. bot. of colony of West. Austr., Trans. of Irish Acad., vol. 22, p. 539; Phyc. austr., pl. 189; Austr. alg., No. 159.

Corynecladia clavata (Sonder) J. Agardh. Epicr., p. 643; De Toni, *l.c.*, vol. 4, p. 810.

Type locality.—Australia.

I have not examined any specimens of Sonder, but have studied Harvey's Australian Algae, No. 159, in a copy preserved in Thuret's herbarium in Paris. In this specimen, the surface cells are sometimes slightly elongated in the cross-section of branchlets, but their arrangement cannot be considered as palisade-like; in Harvey's figure, it seems to me to be slightly modified; in the surface view, they are not projecting, and I could find no lenticular thickenings in the frond.

Laurencia rigida J. Agardh

Plate 18, figure *b*

Epicr., p. 651; De Toni, *l.c.*, p. 789.

Type locality.—The warmer part of Australia.

In the cover of the present species in the herbarium of J. Agardh, there are four sheets and two unmounted small specimens. The first sheet contains Nos. 36688–36690 (No. 36688 is from Max Doneles Bay; No. 36689 is without remark about the locality, and No. 36690 is from Victoria) and on the sheet J. Agardh wrote

"rigida J. Ag.

Laurencia arbuscula Harv.?"

On the second sheet are mounted two kinds of specimens: No. 36691 and Nos. 36692–36693. The former number is from Port Stephen, New South Wales, and is very rigid, and in habit like *L. paniculata* J. Ag.; the latter are from "Ostonary of the Hookeins R." The third sheet contains No. 36694, consisting of four specimens. They are all from "Nov. Holl. boreal.," and most probably represent the type. The fourth sheet contains three numbers: No. 36695 is Harvey's Australian algae No. 340D under the name of *L. papillosa* var.?;

No. 36696 is from "Hamilton Bay Corée) miss Crouan." This Corean specimen seems to me to belong to a quite different species than the present one, having a compressed frond and showing different characters of the surface cells in the branchlets. In this specimen the surface cells are very irregular in shape and arrangement in the cross-section of branchlets, while in *L. rigida* J. Ag. these characters are rather peculiar as will be described below. On the other hand, Yendo referred some Japanese specimens, which agree well with this Corean specimen, to *L. rigida* J. Ag. in his herbarium, probably after having seen the Corean specimen in the Agardhian herbarium. But this does not seem to me to be correct, so I have separated our Japanese specimens from J. Agardh's species and described them as new, naming them as *L. cartilaginea.* Number 36697 came from Max Dounales Bay (miss F. A. Müller), consisting of two specimens. One of the unmounted specimens is No. 36698 and is from Hamilton Bay (Corea). This is also quite different from the type of the present species, most probably the same as what I have named *L. Okamurai.* Another unmounted specimen is very incomplete and without any remark about the locality.

I have studied the anatomical structure of the type (No. 36694). The surface cells are not projecting in the surface view even near the top of the branchlets, are nearly square or slightly elongated radially in the cross-section and making a very distinct layer, which appears somewhat palisade-like. I have found no lenticular thickenings in the walls of the medullary cells. Number 36691 was also examined anatomically; in this specimen, the surface cells are clearly elongated radially in the cross-section of branchlets and disposed like palisade cells; this seems, therefore, to belong to *L. paniculata* J. Ag. In the herbarium of the University of California there are three specimens named by J. Agardh himself, and distributed under his name. I have studied their anatomical structure and found that these three are so different from one another in outer appearance as well as in anatomical structure, that it seems impossible to refer them to one and the same species. The specimen No. 303858 came from New South Wales (Twofold Bay) and has a caespitose habit, showing fibrous roots. It is very low, being about 3 cm. long, probably representing a young stage. In the cross-section, the axis shows clearly the presence of lenticular thickenings in the medullary cells, although they are rather few in number. The surface cells are nearly square or slightly elongated radially and arranged somewhat palisade-like in the cross-section,

though not clearly so. Number 94448 is also a young plant as indicated by J. Agardh himself on the label. This is about 6 cm. high, caespitose with fibrous roots. The surface cells are like those of the preceding specimen. Number 111663 shows a very different habit and the anatomical structure is too peculiar to allow it to be referred even to the genus *Laurencia*.

Laurencia botryoides (Turner) Gaillon

Résumé méth. des class. des thalas., Dict. des sci. nat., vol. 4, p. 15; Harvey, Ner. aust., p. 82; Phyc. austr., pl. 182; J. Agardh, Spec. alg., vol. 2, p. 759; Epicr., p. 658; Kützing, Tab. phyc., vol. 15, pl. 71; De Toni, *l.c.*, p. 802.

Fucus botryoides Turner, Hist., Fuc., pl. 178.

Type locality.—Kent's Island, near Australia.

In this species, the surface cells are neither elongated radially nor arranged like palisade cells in the cross-section of branchlets; in the walls of the medullary cells there are no lenticular thickenings.

In the herbarium of the Royal Botanic Gardens, Kew, there is a specimen of Turner collected by Brown in Australia. Harvey's specimens distributed as the Australian Algae, No. 239, appear to be the same as the above specimen.

The present species stands near *L. cartilaginea* Yam. in outer habit as well as in anatomical character, but it can be distinguished from it by the flexuous frond and its fructified branches densely covered by wart-like ultimate branchlets.

Some specimens from Nagasaki, Japan, now preserved under the name of *L. botryoides* Gaill. in the Martens' herbarium are referable to *L. cartilaginea* Yam. So far as I know, *L. botryoides* Gaill. is limited to Australia.

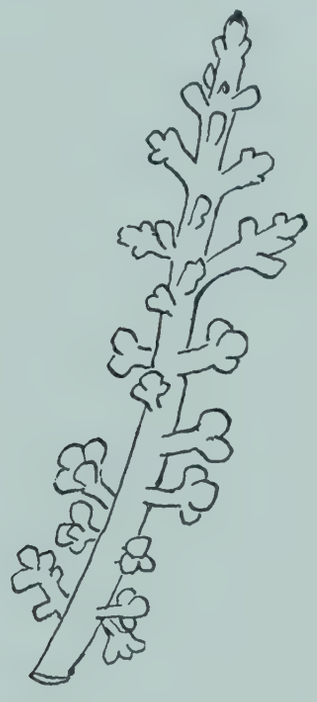
Laurencia cartilaginea sp. nov.

Plate 19, figure *a*; figure O

Radice non fibrosa; fronde 14 cm. alta, ad basin tereti, sed sursum leviter compressa, cartilaginea, mox in ramis primariis decomposita; ramulis secundariis suboppositis; ramulis ultimis brevibus, tuberculiformibus, ad apicem inflatis; cellulis superficialibus ramorum parviorum polygonatis, 39–53μ longis in sectione transversam radiatim leviter elongatis vel interdum rotundatis, non evidenter simili modo ut cellularis valliformibus dispositis; parietibus cellularum medullarum crassis, sed parte crassiori lenticulata non ornatis; stichidiis brevibus, papillaeformibus; cystocarpiis et antheridiis ignotis.

Habitat.—Near Mogi, Prov. Chikuzen; Prov. Iyo, Japan. (Corea in the Herb. of J. G. Agardh).

Root not fibrous; frond about 14 cm. high, cylindrical near the very base, slightly compressed upwards, cartilaginous, soon dividing into a number of primary branches; secondary branches pinnate, nearly distichous, subopposite; ultimate branchlets short, wart-like inflated at apices; surface cells in the shorter branches polygonal, not projecting in the surface view, about 39–53μ long, slightly elongated radially or sometimes rounded, not clearly like palisade cells in the cross-section; the walls of the medullary cells very thick, but without lenticular thickening; stichidia short, wart-like; cystocarps and antheridia unknown.



O. *L. cartilaginea* sp. nov. A small branch. × 3.

The present species appears to be closely related to *L. botryoides* (Turn.) Gaill. on one hand, and to *L. rigida* J. Ag. on the other. But in *L. botryoides* Gaill. the branches are usually flexuous, and wart-like ultimate branchlets cover only the upper parts of the small branches. *L. rigida* J. Ag. has always a cylindrical frond, and that is not the case in the present species.

J. G. Agardh placed a fragmentary specimen of this species in the specific cover of *L. rigida* J. Ag. in his herbarium. His specimen came from Hamilton Bay, Corea, as mentioned above under *L. rigida* J. Ag.

Laurencia Casuarina J. Agardh

Plate 19, figure *b*

Anal. alg., cont. 3, p. 109; De Toni, *l.c.*, p. 781.

Type locality.—Port Elliot, Australia.

The specimens of this species distributed by J. Agardh in the Algae Muellerianae appear to be uniform. I have examined a speci-

men from this origin in the herbarium of Farlow through the kindness of Dr. Dodge, and found that the superficial cells are not projecting in the surface view, are rounded or slightly elongated tangentially and not arranged palisade-like in the cross-section of branchlets. Lenticular thickenings have not been found. In J. G. Agardh's herbarium, Nos. 37006 and 37007 are from Port Elliot (Hussey), so they are the types, but all other specimens in the same cover with the above numbers cannot be distinguished from the type in any way.

Laurencia flexilis Setchell

Tahitian alg., Univ. Calif. Pub. in Bot., vol. 12, p. 101, pl. 19, figs. 1–6.
Laurencia rigens Grunow, in herb.

Type locality.—Tahiti.

In the type specimen (Hb. Univ. Calif. No. 261333), the surface cells are not arranged like palisade cells in the cross-section of branchlets, not projecting in the surface view even near the top of the ultimate branchlets; cell walls are thick; there are no lenticular thickenings in the walls of the medullary cells.

L. flexilis Setch. comes near *L. tropica* Yam. so far as the anatomical structure and substance of the frond are concerned, but can be distinguished by the different branching.

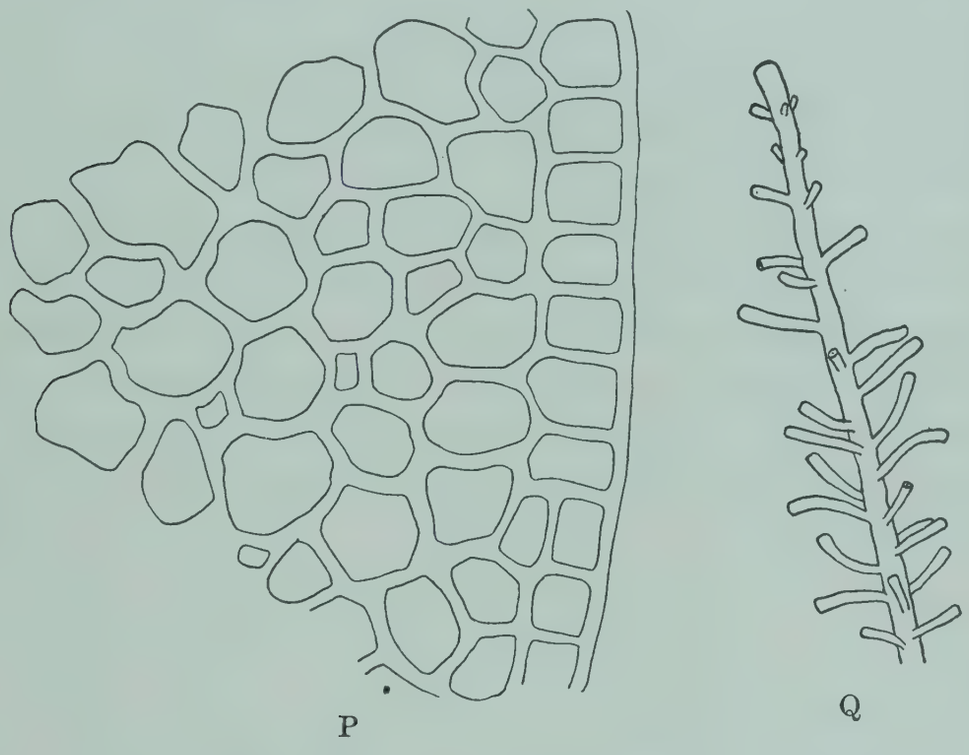
In the Thuret herbarium in Paris, I have seen about seven specimens of *Laurencia* having the name of *L. rigens* Grunow which were collected in Tahiti and sent by Vernier in 1894. Those specimens bear strong resemblance to the type specimen of this species, the frond being very coarse, nearly black in color, and showing about the same branching, especially forming a pyramidal form of branches near the end of the frond as in *L. flexilis* Setch. In anatomical characters Grunow's specimens also agree very well with those of the Tahitian species of Setchell. When I consider that they came from one and the same locality, there seems to be no doubt as to the identity of the specimens in question. However, so far as I have been able to determine, Grunow's name has never been published, so I have adopted Setchell's name.

Some small specimens from Loo-Choo collected by C. Wright in the North Pacific Exploring Expedition are preserved in Cambridge, Massachusetts, Paris, Dublin, etc., under the name of *L. perforata* Mont., but they may be very young stages of this species.

Laurencia tropica sp. nov.

Plate 20; figures P, Q

Radice discum parvum planumque formante; fronde 11 cm. alta, caespitosa, dendroidea, rigida, tereti, subcorymbose ramosa; ramis irregulariter quoquoversum egredientibus patentibus, verticillatis vel alternis; ramulis sursum corymbosis; ramulis ultimis cylindraceo-clavatis, 2–3 mm. longis, ad apices truncatis, ad inferiorem partem ramulorum saepe dividuis, dense quoquoversum egredientibus, axillis patentissimis, lineamentum obelisci formantibus; cellulis superficialibus in sectione transversa saepe tangentialiter elongatis, ca. 26–35μ longis, 20–26μ latis, parietibus cellularum medullarum crassis, sed parte incrassata lenticulata non ornatis; cystocarpiis infra apicem ramulorum ultimorum inflatis; tetrasporangiis et antheridiis ignotis; colore fusco-livido, sicco nigrescenti.



P. *L. tropica*, sp. nov. The type specimen. × ca. 330. A cross-section of a branchlet.

Q. *L. tropica* sp. nov. The top of a branch. × ca. 2.

Habitat.—Saipan, Marianna Islands; Kōtōshō, Formosa?

Root a small flat disk; frond about 11 cm. high, caespitose, dendroid, rigid, dark blueish, turning blackish on drying, cylindrical, much branched, branching rather irregular in every direction, patent, sometimes verticillate, sometimes alternate, branchlets corymbose upwards; ultimate branchlets closely arranged, simple or sometimes, especially in the lower parts of the branchlets, divided, issuing in every direction and at very wide angles, forming an obelisk-like outline, clavate, truncate at apices, 2–3 mm. long; cell walls thick, surface cells not elongated radially in the cross-section, but often

elongated tangentially, about 36–35μ long, 20–26μ broad; no lenticular thickenings in the walls of the medullary cells; cystocarps borne on the sides of the ultimate branchlets below the apex; stichidia and antheridia unknown.

As mentioned above, this species comes very near to *L. flexilis* Setch. in texture as well as in anatomical structure, but the branching is very different in these plants, and since I have not met with any intermediate form, I have described it as a distinct species. Possibly it may have to be reduced to *L. flexilis* Setch. after obtaining many more specimens from different localities.

Laurencia tasmanica Hooker et Harvey

Plate 21

Harvey's Ner. austr., p. 84; J. Agardh, Spec. alg., vol. 2, p. 755; Epicr., p. 654; De Toni, *l.c.*, p. 795.

Laurencia excelsa Kützing, Tab. Phyc., vol. 15, pl. 63.

Type locality.—Tasmania.

I have seen several specimens of this species distributed by Harvey under Australian Algae No. 238 in many herbaria which seem to be uniform. In these specimens the surface cells are not projecting in the surface view even at the top of the branchlets, neither are they elongated radially nor arranged like palisade cells in the cross-section of branchlets; there are no lenticular thickenings in the walls of the medullary cells.

Laurencia regia Harvey

Plate 22, figure *a*

Austr. alg., exss., No. 237.

Laurencia obtusa var. *regia* Harvey, Phyc. austr. Syn., No. 309*a*.

Type locality.—Australia.

I have examined specimens of the Australian Algae No. 237 distributed by Harvey in several herbaria. The plants of this number have no lenticular thickenings, and the surface cells are neither elongated radially nor arranged like palisade cells in cross-sections of branchlets, and they are not projecting in the surface view. The frond is usually cartilaginous and often shows distichous branchlets with the stichidial branchlets usually cymosely or paniculately compounded.

Harvey at first considered this plant to be an independent species, but afterward reduced it to a variety of *L. obtusa* Lamx. But, because

of its branches often being distichous and of its compound stichidial branchlets, it seems better to separate it specifically from *L. obtusa* Lamx. On the other hand, this species shows some resemblance to *L. tasmanica* Harv., though it is not so robust as that species.

Laurencia distichophylla J. Agardh

Spec. alg., vol. 2, p. 762; Epicr., p. 656; Harvey, Flor. nov. Zel., p. 234; De Toni, *l.c.*, p. 800.

Type locality.—Cape of Good Hope?

In the cover of the present species in the Agardhian herbarium, there are two sets of specimens as to locality of collection: some specimens are from New Zealand (collected by Berggren), while two specimens are "an e Cap. b. Spei (Hab. Ag.)," and they are Nos. 37170 and 37171. Number 37171 is a very nice specimen, being about 7 cm. high, flattened in frond, about 1.5 mm. wide in the widest part, distichously pinnately branched, branches often *alternate!* with round angles and with stichidial branchlets arranged corymbosely. As to the interior of the frond, there are no thickenings, at least, near the end of the branches; the surface cells are neither elongated radially, nor arranged like palisade cells in the cross-section of branchlets. They do not project in surface view.

Laurencia corymbosa J. Agardh

Plate 22, figure *b*

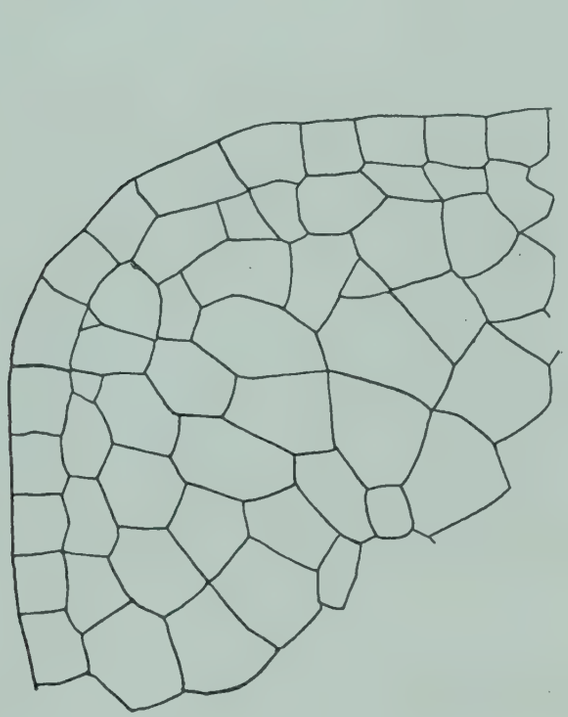
Spec. alg., vol. 2, p. 716; Epicr., p. 648; De Toni, *l.c.*, p. 783.

Type locality.—Cape of Good Hope.

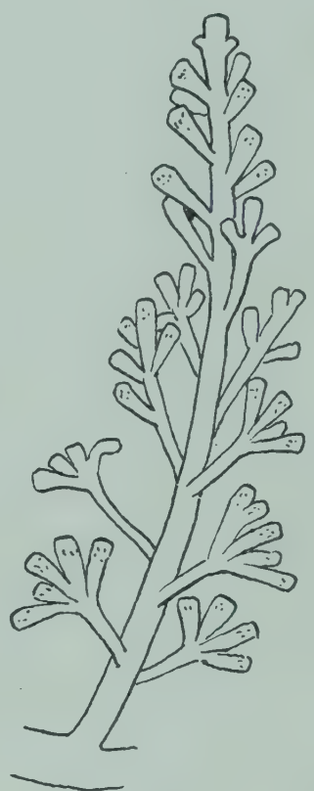
In the herbarium of J. Agardh, there are three specimens under the present specific name: No. 36607 is rather fleshy, adhering closely to the paper; No. 36608 was sent from the Museum of Paris and on the label accompanying it is a remark, reading: "*F. obtusa* aff. Ass. Delaland," so most probably this number is the type specimen; No. 36609 is represented by two small specimens having the name of *Chondria obtusa* var. *gracilis* Ag.

In No. 36608, there are no lenticular thickenings near the top of the branchlets. The cell walls are thin, but below they become very thick and often, even the wall of the surface cells, is evidently thickened on the outside. The surface cells are neither elongated radially, nor disposed like palisade cells in cross-sections of branchlets, and in the surface view they are not projecting.

In the herbarium of the National Museum of Natural History in Paris, there are two specimens of this species, one of which was collected by Lalande at the Cape of Good Hope and determined by Bornet. This specimen shows exactly the same habit and about the same anatomical structure as the type specimen at Lund, but near the base there are some lenticular thickenings in the walls of the medullary cells. The other specimen was communicated by J. G. Agardh and the specific name is written in his handwriting.



R



S

R. *L. composita,* sp. nov. × ca. 330. A cross-section of a small branchlet.

S. *L. composita* sp. nov. A small branch. × 6.

Laurencia composita sp. nov.

Plate 23; figures R, S

Radice fibrosa?; fronde 10 cm. alta, tereti, 1–2 mm. crassa, enormiter pinnatim quoquoversum ramosa; ramis longis, ramulo longissimo 8 cm. attingente, iterum pinnatim ramosis; ramulis comparate brevibus, 3–10 mm. longis, alternis vel suboppositis, paniculatis; ramulis ultimis tetrasporangiiferis cylindraceo-clavatis, ad apices leviter rotundatis, paniculatim aut corymbose fasciculatis; cellulis superficialibus parvis, forma et dispositione irregularibus; parte incrassata lenticulata cellularum medullarum non adeunti; cystocarpiis et antheridiis ignotis; colore sicco nigrescenti.

Habitat.—Enoshima, Prov. Sagami; Mera, Prov. Bōshū, Japan.

Root fibrous?; frond 10 cm. high or more, cylindrical, 1–2 mm. thick, irregularly pinnately branched; branches long, the longest one attaining about 8 cm., issuing on every side of the main axis; branchlets again pinnately branched, comparatively short, up to 1 cm. long, alternate or subopposite, paniculate; ultimate branchlets bearing tetrasporangia cylindrical-clavate, slightly rounded at the apices, paniculately or cymosely fasciculated; surface cells small, not palisade-like; there are no lenticular thickenings in the walls of the medullary cells; cystocarps and antheridia unknown.

This new species resembles the figure of *L. cymosa major* Kg. from the Cape of Good Hope in Tabulae Phycologicae, but can be distinguished from it by the ramification; this Kützing species seems to me to be the same as *L. virgata* J. Ag. It bears some resemblance also to *L. Yendoi* Yam., having decompound stichidia, but in the latter species the surface cells are larger than those of the parent species and the arrangement of stichidial clusters is very different from that of *L. Yendoi* Yam.

Laurencia Yendoi sp. nov.

Plate 24

Fronde caespitosa, 25 cm. alta, leviter compressa, 2–3 mm. crassa, axi principali percurrenti enormaliter pinnatim ramoso; ramis iterum pinnatim ramosis, quoquoversum egredientibus, elongatis cum brevioribus mixtis, patentibus; ramulis obelisciformibus; ramulis ultimis clavatis, ad apices plerumque truncatis; tetrasporangiiferis cymose fasciculatis, deinde spiraliter ad ramulos ultimos dispositis; cystocarpiis abundanter ad quod latus ramulorum ultimorum gerentibus; cellulis superficialibus forma inaequalibus, in sectione transversa rotundatis vel tangentialiter elongatis; parietibus cellularum medullarum parte incrassata lenticulata non ornatis.

Laurencia heteroclada Yendo (non Harvey), Notes on alg. new to Japan, vol. 6, p. 89 (Tokyo Bot. Mag., vol. 31, 1916).

Habitat.—Hidaka, and Rishiri-tō, Hokkaido; ?Onabama, Prov. Iwaki, Japan.

Frond caespitose, 25 cm. high, slightly compressed, fleshy, 2–3 mm. thick, principal axis percurrent, irregularly pinnately branched, irregularly placed, mixing long branches with shorter ones, patent; lesser branches of obelisk-like outline; ultimate branchlets clavate, in most cases truncated at apices; stichidia cymosely fasciculated and these fascicles closely spirally arranged on the lesser branchlets; cystocarps abundant, produced on every side of the ultimate branchlets; surface cells irregular in shape, sometime rounded; sometimes elongated tangentially in the cross-section; without the lenticular thickenings in the walls of the medullary cells.

The specimens on which I have established this new species were referred by Yendo to *L. heteroclada* Harv. I have examined his

specimens and have come to the conclusion that it is not desirable to identify them with the Harvey species. Although in both specimens from Australia and Japan, the stichidial branchlets are compounded, their arrangement is quite different from one another, so that I have described our specimens as new, dedicating the species to the late Professor K. Yendo.

Laurencia heteroclada Harvey

Acc. of Mar. bot. of colony of West. Austr., Trans. Irish Acad., vol. 22, p. 544, Phyc. austr., pl. 148; J. Agardh, Epicr., p. 647; De Toni, *l.c.*, p. 782.

?Laurencia arbuscula Sonder, Alg. Preis., p. 55 (Bot. Zeitung, 1845).

Type locality.—Australia.

Harvey's Australian Algae No. 234*a* under the name of the present species has been examined in the herbarium of Thuret in Paris. In this specimen the surface cells are slightly elongated radially in the cross-section of branchlets, but this character is not so clear as it is shown in the figure of Harvey in Phycologia australica.

In the herbarium of Dr. Okamura, there is a specimen collected in the Province Iyo, Japan, by Mr. Ogata which is most safely referable to the present species, although the specimen is fragmentary. On the other hand, Yendo referred some specimens from Hokkaido to the present species which I have described above as *L. Yendoi.*

L. arbuscula Sond. from Australia was reduced to a synonym of *L. heteroclada* Harv. by J. Agardh in Epicrisis. In the Agardhian herbarium at Lund, there are some specimens in the cover of this species of which No. 36559 was collected by Preiss in "Nov. Holl. austro-occid" and is from Herbarium Binder. This specimen is about 4 cm. long, being slightly smaller than the other specimens. Another specimen from the same source is preserved in the herbarium of von Martens which is to be found in Berlin-Dahlem. In this specimen, the surface cells are not arranged like palisade cells in the cross-section of branchlets, not projecting in the surface view, and there are no lenticular thickenings in the walls of the medullary cells, so far as I have examined.

Laurencia estebaniana Setchell et Gardner

Exped. of Calif. Acad. of Sci. to Gulf of Calif., Proc. Calif. Acad. Sci., vol. 4, p. 763, pl. 24, fig. 34, pl. 45*a*.

Type locality.—Gulf of California

I have examined the cotype specimen of this species in Berkeley. The surface cells are not projecting in the surface view, neither are they elongated radially, nor disposed like palisade cells in cross-sections of branchlets. In the walls of the medullary cells I have never met with any lenticular thickenings, but instead there are some yellow, gland-like cells among the medullary cells.

Section Pinnatifidae

Frond clearly compressed, branching almost always pinnate; surface cells scarcely elongated radially and not arranged like palisade cells in cross-sections of branchlets; lenticular thickenings in the walls of the medullary cells not common.

I have grouped here all species which show the fronds clearly flattened. Some of them possess lenticular thickenings in the walls of the medullary cells, but usually these are not abundant, e.g., in *L. pinnatifida* Lamx. they are limited only to the basal part of the frond.

Laurencia sinicola Setchell et Gardner

Exped. of Calif. Acad. of Sci. to Gulf of Calif. mar. alg., Proc. Calif. Acad. Sci., vol. 4, p. 764, pl. 29, figs. 65–66, pl. 50*a*.

Type locality.—Gulf of California.

In the herbarium of the University of California, Johnston's No. 126 and Marchant's No. 34 have been studied. In these specimens, there are many lenticular thickenings in the walls of the medullary cells, but the former specimen shows many more than the latter. The surface cells of branchlets are not projecting in the surface view, neither are they elongated radially nor arranged like palisade cells in cross-sections of branchlets.

Laurencia pinnatifida (Gmelin) Lamouroux

Ess. sur gen. de fam. des thalas., p. 42; Greville, Alg. brit., p. 108, pl. 14 (except var. *angusta* Turner); Kützing, Spec. alg., p. 856; Tab. phyc., vol. 15, pl. 66, figs. *a-f*; Harvey, Phyc. brit., pl. 14, figs. 1–5; J. Agardh, Spec. alg., vol. 2, p. 764; Epicr., p. 656; De Toni, *l.c.*, p. 798.
Fucus pinnatifidus Gmelin, Hist. Fuc., p. 156, pl. 16, fig. 3; Turner, Hist. Fuc., pl. 20.

Type locality.—France?

In the principal branches of well grown specimens of this species, the lenticular thickenings are found very often. A specimen from Calvados determined by Lamouroux as the present species, is pre-

served in the herbarium of Thuret in Paris. In the principal branches, I have found several lenticular thickenings, and the same thing has been my experience in fresh specimens at Sant-Servan, France.

As to the distinction from *L. spectabilis* Post. et Rupr. I shall give some notes under *L. spectabilis*.

Laurencia Brongniartii J. Agardh

Plate 25, figures *a*, *b*

In historiam alg. symbolae, Linnaea, vol. 15, p. 20, 1841; J. Agardh, Spec. alg., vol. 2, p. 768; Epicr., p. 660; De Toni, *l.c.*, p. 805.

Laurencia concinna Montagne, Prodr. phyc. ant., p. 6; Voy. pol. sud., p. 126, pl. 14, fig. 3; J. Agardh, Spec. alg., vol. 2, p. 764; Epicr., p. 661; De Toni, *l.c.*, p. 806.

Type locality.—The Martinique Islands.

The type specimen of *L. Brongniartii* J. Agardh is probably No. 37257 in the Agardhian herbarium, because this number is the only specimen at Lund sent by Brongniart and collected in the Martinique Islands. The frond of this specimen is about 18 cm. long, with a percurrent thick axis from which issue many branches irregularly pinnately; the branches are clearly flattened, showing midribs in the lower part; the ultimate branchlets are rather long and inflated at the top, almost always simple. The surface cells are not projecting in the surface view and are not arranged like palisade cells in the cross-section of branchlets. There are some lenticular thickenings in the walls of the medullary cells, although not abundant.

In the general herbarium in Paris there is a specimen of this species which belonged to the herbarium of Brongniart, so most probably a cotype specimen. In every respect it coincides very well with the type specimen at Lund.

In the herbarium of Montagne, there is a specimen of *L. concinna* Mont. which was collected by d'Urville at "Ile Toud," so it is undoubtedly the type specimen of Montagne's species. In this specimen the frond is about 5.5 cm. high, compressed, 2 mm. wide in the widest part (in the dried condition); branches alternate toward the base and often as well toward the top, strongly patent, sometimes rectangular to the principal branches; stichidial branchlets clavaeform, strongly rounded at the top, simple or compound. The surface cells do not project in the surface view even at the end of the ultimate branchlets. In the cross-section of branchlets, the cells are nearly quadrate in shape, not arranged like palisade cells, very small compared with the outermost cells of the medulla; medullary cells show lenticular thick-

enings in their walls, although not abundantly. Color yellowish red, adhering to the paper imperfectly.

The specimens distributed by J. Agardh under the name of *L. concinna* Mont. as "Alg. Muell." seem also to belong to this species. I have examined one specimen which came from "Port Douglas, Nov. Holl. Subtropca." in the herbarium of Thuret in Paris. This specimen shows strong resemblance with the type of *L. concinna* Mont. in external habit as well as in anatomical characteristics. Another specimen under the name of *L. calliptera* Kg. collected by Vieillard in New Caledonia is preserved in the same herbarium as the above specimen. This specimen agrees rather well with the type specimen of *L. concinna* Mont. although its frond is slightly narrower and shows more lenticular thickenings than does the type specimen of Montagne.

Having compared all specimens mentioned above, I have come to the conclusion that they all should be considered as belonging to one and the same species, whose name, according to the rule of the priority, must be *L. Brongniartii* J. Ag.

Laurencia elata (C. Agardh) Harvey

Plate 26, figures *a*, *b*; plate 27

Ner. austr., p. 81, pl. 33; Phyc. austr. syn. No. 331; J. Agardh, Spec. alg., vol. 2, p. 766; Epicr., p. 659; Kützing, Tab. Phyc., vol. 15, pl. 67, figs. *d-g;* De Toni, *l.c.*, p. 803.

Chondria pinnatifida var. *elata* C. Agardh, Spec. alg., vol. 1, p. 340; Sonder, Alg. Preis., Bot Zeitung, p. 30, 1845.

Type locality.—King Island, near Australia.

In the general herbarium in Paris, there is the type specimen of *Chondria pinnatifida* var. *elata* C. Ag. which was quoted by C. Agardh in Species algarum. It is about 24 cm. long without the root. Its surface cells are not arranged like palisade cells in the cross-section of branchlets, and in the walls of the medullary cells of large branches there are lenticular thickenings.

At Dublin, I have seen also the specimen of Harvey which was collected by Gunn in Tasmania, and which was figured by Harvey in the *Nereis australis.* There is no difference between the two specimens.

The present species comes rather near *L. pinnatifida* Lamx. but can be easily separated by the differences in branching. Under this species two forms may be distinguished.

Forma **luxurians**

Laurencia elata var. *luxurians* Harvey, Phyc. austr. syn., No. 313*a*.
Laurencia luxurians (Harvey) J. Agardh, Epicr., p. 658; De Toni, *l.c.*, p. 804.

Type locality.—Australia.

In this form, the frond is more densely branched than in the species and in another form, and is rather soft. It is also noticeable that in many cases, the specimens referable to the species are cystocarpic, while the specimens of form *luxurians* are mostly tetrasporic.

Forma **flexuosa** Kützing

Spec. alg., p. 856; Tab. phyc., vol. 15, pl. 68; J. Agardh, Spec. alg., vol. 2, p. 767; Epicr., p. 658; De Toni, *l.c.*, p. 802.

Type locality.—Cape of Good Hope.

In the herbarium of J. G. Agardh at Lund, Nos. 37212 and 37213 were collected by Pappe at Cape of Good Hope; in various other herbaria I have seen a considerable number of specimens under *L. flexuosa* Kg. and have come to the conclusion that this plant does not differ sufficiently to be distinguished specifically or even varietally from *L. elata* Harv.

J. Agardh states that in *L. flexuosa* Kg. the branching is more pinnate than it is in *L. elata* Harv., thus approaching to *L. pinnatifida* Lamx. But this character does not appear to be strong enough to separate it specifically from *L. elata* Harv.

Laurencia pinnata sp. nov.

Plate 28

Fronde 11 cm. alta, ad basin teretiuscula, sursum mox complanata, membranacea, 2 mm. lata, in ramos primarios decomposita; ramis primariis pinnatim ramosis; ramulis secondariis e margine ramorum primariorium exeuntibus, alternis vel suboppositis, patentibus, axillis rotundatis, iterum pinnatim ramosis; ramulis ultimis breve clavatis, ad apices truncatis vel leviter rotundatis; tetrasporangiis in ramulis ultimis conformibus situatis; cellulis superficialibus in partibus superioribus ramulorum leviter projicientibus, ramulis primariis rotundatis vel tangentialiter pauce elongatis ad sectionem transversam partem crassiorem lenticulatam cellularum medullarum gerentibus; cystocarpiis et antheridiis ignotis; colore rubro-purpureo, substantia molli.

Habitat.—Enoshima, Province Sagami, Japan.

Frond about 11 cm. high, cylindrical near the base, soon complanated upwards, about 2 mm. wide, membranaceous, dividing into

a number of primary branches; primary branches pinnate; secondary branches issuing from the margins of the primary branches, alternate or subopposite, patent with round axils, in turn pinnate; ultimate branchlets shortly clavate, truncated or slightly rounded at apices, tetrasporangia distributed on the similar ultimate branchlets; cystocarps and antheridia unknown; surface cells in the upper parts of the frond projecting, though not very strongly so, those in the primary branches rounded or slightly elongated tangentially in the cross-section; no lenticular thickenings present in the walls of the medullary cells.

In this species the texture is rather soft and the color is reddish-purple, and, as described above, the surface cells in the upper parts of the frond are projecting, though not so clearly as in *L. mariannensis.*

C. Wright's specimens, collected at Hakodate in the North Pacific Exploring Expedition and named by Harvey as *L. pinnatifida* Lamx., is most probably the same as this species, being neither *L. pinnatifida* Lamx. nor *L. spectabilis* Post. et Rupr.



T. *L. undulata* sp. nov. The top of a branch. × 1.5.

Laurencia undulata sp. nov.

Plate 29, figure *a*; figure T

Radice discum planum formanti; fronde caespitosa, complanata, sursum dilatata, 5 mm. lata, bipinnatim sparsim ramosa; ramis e margine distiche ramosis, axillis rotundatis; ramulis ultimis ad apices truncatis vel rotundatis, sursum leviter curvatis; cellulis superficialibus quadrangulatis in sectione transversa radiato, leviter elongatis 26–32μ latis; partem incrassatam lenticulatam ad parietes cellularum medullarum non ostendentis; cystocarpiis ad marginem verrucosam undulatam ramulorum ultimorum numerosis; tetrasporangiis et antheridiis ignotis.

Habitat.—Enoshima, Province Sagami, Japan.

Root a flattened disc; frond caespitose, complanate, dilatate upwards up to about 5 mm. wide, bipinnately branched, branching infrequent, branches distichous, axils not broad but rounded, ultimate branchlets truncated or rounded at the apices, slightly curved upward; surface cells quadrangular, slightly elongated radially in the cross-section, 26–32μ long, 18–26μ broad; no lenticular thickenings present in the walls of the medullary cells; cystocarps numerous on the margins of the ultimate branchlets forming verrucose, ruffled outline; stichidia and antheridia unknown.

The present species belongs undoubtedly to the section *Pinnatifidae* of J. Agardh and among its species *L. spectabilis* Post. et Rupr. appears to have some resemblance to the present species, but the verrucose ruffled margins in the fertile condition of our species is so characteristic that they are easily separable from one another.

L. undulata seems to be very variable in outer form, often producing very irregular, complicated outline.

Laurencia botrychioides Harvey

Plate 29, figure *b*

Flora Nov. Zel., p. 234; J. Agardh, Epicr., p. 657; De Toni, *l.c.*, p. 802.

Type locality.—New Zealand.

J. Agardh considered that the present species is a young form of *L. distichophylla* J. Ag., and Yendo followed him. In the herbarium of Harvey at Dublin and also in the herbarium at Kew, there are several specimens of this species collected by Colenso in New Zealand. Having compared these specimens with J. Agardh's specimens of his species, it seems to me to be preferable to keep the Harvey species distinct from L. *distichophylla* J. Ag. unless we find other specimens linking sufficiently the two species, even though they stand in a very close relation.

Laurencia ceylanica J. Agardh

Plate 30, figure *a*

Epicr., p. 660; De Toni, *l.c.*, p. 805.
Laurencia sp. Harvey's Ceylon Alg., No. 17.
Laurencia pectinata Greville, in herb.

Type locality.—Ceylon.

Harvey's Ceylon Algae, No. 17, was examined in the herbarium of Thuret in Paris. It has surface cells radially elongated in cross-sections of branches and these are arranged somewhat palisade-like,

but in the surface view they are quite smooth. There are no lenticular thickenings in the walls of the medullary cells. The most characteristic feature of the present species is the very short tuberculate ultimate branchlets, which indicates at once the present species.

In the Agardhian herbarium, there are also two specimens (on one sheet), Nos. 37261 and 37262. Both are Harvey's Ceylon Algae, No. 17, and are the same as other specimens of this number of Harvey kept in Paris. In the herbarium of the Royal Botanic Gardens, Edinburgh, there are preserved the specimens of Greville, among which I have found one sheet of *Laurencia* containing five specimens. They are named by Greville as *L. pectinata* Grev. On the accompanying label, there is a note reading: "Herb. Wight prop. Cryptogamea Peninsula Ind. orientalis," and they are exactly the same as Harvey's Ceylon Algae, No. 17, viz., *L. ceylanica* J. Ag. So far as I have been able to consult the literature, this name of Greville has never been published. In the herbarium of Harvey, this number of Ceylon Algae is preserved among the unnamed specimens and there are several specimens on one sheet but this number seems to be uniform and to represent a good species. In the herbarium in Paris, I have seen a copy of Ferguson's Ceylon Algae, No. 27, and this, also, appears to belong to the present species. In the herbarium of Okamura, there is a specimen from Shikoku which is referable also to *L. ceylanica* J. Ag.

Laurencia Grevilleana Harvey

Acc. of mar. bot. of colony of West. Austr., Trans. of Roy. Irish Acad., vol. 22, p. 545; Phyc. austr., pl. 15; J. Agardh, Epicr., p. 661; De Toni, *l.c.*, p. 806.

?Laurencia concinna Okamura (non Montagne), Icon. of Jap. Alg., vol. 2, p. 38, pl. 40, figs. 1–6.

Type locality.—Rottnest Island, Western Australia.

In several herbaria including that of Harvey, I have studied the type specimen as well as the authentic specimens of this species. The surface cells are not disposed like palisade cells in the cross-section, are not projecting in the surface view, and there are no lenticular thickenings in the walls of the medullary cells.

As was noticed by Harvey, *L. Grevilleana* Harv. shows a rather soft frond and is easily separated by this character from *L. Brongniartii* J. Ag.

Okamura gave good figures of a Japanese plant which he referred to *L. concinna* Mont. I have also some specimens from the southern

part of Japan which appear to be the same as his plant. From the texture of the frond, and from other characteristics, it seems to me to be more reasonable to refer it to the present species than to *L. concinna* Mont. The Japanese specimens, however, very often show opposite branches, while in *L. Grevilleana* Harv. they are usually alternate, and I wonder whether the former specimens may be nothing but a form showing more condensed branches rather than the typical form of the latter.

Number 319 of the American Algae distributed by Tilden under the name of *L. Grevilleana* Harv. does not seem to me to be a *Laurencia*.

Laurencia spectabilis Postels et Ruprecht

Illust. alg. Ocean. Pac., impr. sept., p. 16; J. Agardh, Spec. alg., vol. 2, p. 764; Epicr., p. 656; De Toni, *l.c.*, p. 799.

Laurencia californica Kützing, Spec. alg., p. 857; Tab. phyc., vol. 15, pl. 67, figs. *a-c*.

Type locality.—West coast of North America.

After examining several authentic specimens distributed by Ruprecht under the present specific name in the Farlow herbarium at Cambridge, Massachusetts, in Paris, and in the Agardhian herbarium at Lund, and also after observing the living plant on the shore of California, I have come to the conclusion that the present species is to be separated from *L pinnatifida* Lamx. As has been stated above, I have also personally collected specimens of *L. pinnatifida* Lamx. in France, and have found that in *L. pinnatifida* Lamx. there are often the lenticular thickenings in the walls of the medullary cells near the base of the frond, which are never found in plants of the California species.

As has been noticed by the American phycologists, there are two forms under the present species in California, a broader form and a narrow and rather cartilaginous form, but they do not seem to me to be different specifically, one from the other. A specimen, No. 37150, in the Agardhian herbarium is preserved in the cover of *L. spectabilis* Post. et Rupr. This specimen was collected by C. Wright at Hakodate, Japan, and referred by Harvey to *L. pinnatifida* Lamx., but most probably it belongs to *L. pinnata* Yam. and I doubt the occurrence of *L. spectabilis* Post. et Rupr. in Japanese waters.

Laurencia thyrsifera J. Agardh

Plate 30, figure *b*

Epicr., p. 654; De Toni, *l.c.*, p. 795.

Type locality.—Chatham Island.

In the cover of the present species in the Agardhian herbarium at Lund, there are six specimens from one and the same locality, "the Chatham Islands, 1872 Travers, sub no. 4" of which three complete specimens are mounted on one sheet (No. 36976), while the others are not mounted (No. 36977). They are both in the cystocarpic and tetrasporic condition. The root is fibrous. The frond shows a principal percurrent flattened stem. The branching is almost always distichous, pinnate-paniculate, with branches opposite or alternate. It is dark red in color. The surface cells are irregular in shape in the cross-sections of branches, sometimes elongated tangentially, sometimes radially, but not arranged like palisade cells. Lenticular thickenings are present in the walls of the medullary cells.

In the herbarium of the Royal Botanic Gardens, Kew, there is a specimen under the name of "*L. obtusa* var." collected by Miss Smith in Little Island, New Zealand, in 1907, which is referable to the present species.

LITERATURE CITED

Agardh, C.
1822. Species algarum rite cognitae, vol. 1 (part 2).
1824. Systema algarum.

Agardh, J. G.
1841. In historiam algarum symbolae (Linnea, vol. 15).
1863. Species, genera et ordines algarum, vol. 2.
1876. Epicrisis Floridearum.
1892. Analecta algologica. Observations de speciebus algarum minus cognitis earumque dispositione. (Continuatio 3. 1896.)

Börgesen, F.
1918. Marine algae of the Danish West Indies, vol. 2.
1924. Marine algae from Easter Island (Extract from Nat. Hist. Juan Fernandez and Easter Island).

Bory de St. Vincent.
1803. Essai sur les iles Fortuniees.
1826. Dictionaire class. d'histoire naturelle, vol. 9.

Cotton, A. D.
1912. Clare Island Survey, Pt. 15, Marine algae. Proc. Roy. Irish Acad., vol. 31.

De Candolle, A. P.
1805. Flora Française, vol. 2.

De Toni.
1903. Sylloge algarum omnium hucusque cognitarum, vol. 4, 1903.
1924. *Idem.*, vol. 6.

De Toni, Forti et Howe.
1920. Atti R. Instituto Veneto, vol. 97.
1921. A new species of Laurencia from Chile described by De Toni, Forti and Howe: Laurencia chilensis, sp. nov. (La Nuova Notarisia).

Falkenberg, P.
1901. Die Rhodomelaceen des Golfes von Neapel und der angrenzenden Meeresabschnitte.

Forskaal, P.
1775. Flora Aegiptico-arabica.

Gaillon, B.
1828. Résumé méthodique des classifications des Thalassiophytes. Dict. des sciences naturelles, vol. 4.

Gmelin, S. G.
1768. Historia Fucorum.

Greville, R. K.
1830. Algae britannicae.

Grunow, A.
1867. Reise seiner Majestät Fregatte Novara um die Erde. Bot., Teil 1, Bd. Algen.
1874. Algen der Fidschi- Tonga- und Samoa-Inseln, gesammelt von Dr. E. Graeffe. Jour. des Mus. Godeffroy, Heft 6.

Harvey, W. H.
1847–49. Nereis Australis or Algae of the Southern Ocean.
1849–51. Phycologia britanica.
1853. Nereis boreali-americana, vol. 2.
1854. Some account of the marine botany of the colony of Western Australia. Trans. of the Roy. Irish Acad., vol. 22.
1855. Flora novae Zealandicae.
1858–63. Phycologia australica.

Hauck, F.
1888. Ueber einige von Hildebrandt im Roten Meere und Indischen Ozean gesammelte Algen, Hedwigia, vol. 27.

Howe, M. A.
1905. Phycological studies, II. Bull. Torr. Bot. Club, vol. 32.
1918. Flora of Bermuda (Britton's Flora of Bermuda).
1920. Bahama Flora (Britton and Millspaugh's Bahama Flora).

Hudson, G.
1778. Flora anglica (ed. 2).

Kützing, F. T.
1843. Phycologia generalis.
1845. Phycologia germanica.
1849. Species algarum.
1865. Tabulae phycologicae, vol. 15.

Kylin, H.
1923. Studien über die Entwicklungsgeschichte der Florideen. K. Sv. Vet. Acad. Handl., Bd. 63.
1925. The marine red algae in the vicinity of the Biological Station at Friday Harbor, Wash. Lunds Univ. Årsskr., vol. 2:21.
1928. Entwicklungsgeschichtliche Florideenstudien. *Ibid.*, vol. 2:24.

Lamouroux, J. V.
1805. Dissertations sur plusieurs especes de Fucus.
1813. Essai sur les genres de la famille des Thalassiophytes non articulées.

Lenormand.
1830. In Duby's Botanicon Gallicum seu synopsis plantarum in flora Gallica descriptarum. II. Plant. cell. seu acot.

Lucas, A. H. S.
1919. Notes on the Australian marine algae. II.

Montagne, C.
1838–42. Historie physique, polityque et naturelle de l'ile de Cuba. Botanique Plant. cell.
1840. Histoire naturelle des iles Canaries. Phytographia canariensis sectio ultima.
1842–45. Voyage au pole sud et dans l'oceanie, executé part les corvettes l'Astrolabe et la Zelee. Plantes cell.

Okamura, K.
1909. Icones of Japanese algae, vol. 2.
1916. Nippon Sorui Meii (ed. 2).

Pilger, R.
1920. Algae Mildbraed Annobonensis. Engler's Botan. Jahrb., Bd. 57.

Postels, A., et Ruprecht, F. J.
1840. Illustrationes algarum Oceani Pacifici imprimis septentrionalis.

Schmitz, F.
Florideae (Engler and Prantl's Natürliche Pflanzenfamilien).

Setchell, W. A.
1914. Parasitic Florideae. I. Univ. Calif. Pub. in Bot., vol. 6.
1926. Tahitian algae. *Ibid.*, vol. 12.

Setchell, W. A., and Gardner, N. L.
1924. Expedition of the California Academy of Science to the Gulf of California. Proc. of Calif. Acad. Sci., vol. 4.

Sonder, W.
1845. Algae Preissianae. Bot. Zeit.
1852. Plantae Müllerianae. Linnea, vol. 25.

Turner, D.
1808–1819. Fuci (commonly quoted as *Historia fucorum*).

Velley, T.
1795. Colored figures of marine plants.

Weber-van Bosse, A.
1913. Marine algae of Sealark expedition. Trans. Linn. Soc. Bot., vol. 8.
1923. Liste des algues du Siboga, vol. 3.
1928. Algues de l'expédition danoise aux îles Kei.

Yendo, K.
1915. Notes on algae new to Japan, V and VI. Tokyo Bot. Mag., vols. 30
1916. and 31.

Zanardini, J.
1872. Phycearum indicarum pugillus.

EXPLANATION OF PLATES

PLATE 1

a. L. papillosa (Forsk.) Grev. The type specimen of *Fucus papillosus* Forskaal in the herbarium of Forskaal. × 8/11.

b. L. papillosa (Forsk.) Grev. An authentic specimen (the type specimen?) of *L. cyanosperma* Lamx. in the herbarium of Lamouroux. × ¾.

c. L. intermedia sp. nov. A cotype specimen, young. Slightly magnified.



a



b



c

PLATE 2

L. intermedia sp. nov. The type specimen. × 25/28.



PLATE 3

a. L. paniculata J. Ag. The type specimen of *Chondria obtusa* var. *paniculata* C. Ag. No. 36711 in the herbarium of J. Agardh. × 8/11.

b. L. perforata (Bory) Mont. The type specimen of *Fucus perforatus* Bory in the Thuret herbarium. × ca. 1.



a



N. Fucus perforatus. Mai sur les Obs sot. p. 305. * de ce titre les morceaux figurés. pl. V. f. 5. (N.° 6. du premier au dessus des trous des rochers de la rade de Ste. Croix datés

b

PLATE 5

a. L. cruciata Harv. An authentic specimen in the herbarium of Harvey. × 1.

b. L. mariannensis sp. nov. The type specimen, slightly reduced.



a



b

PLATE 6

a. L. venusta sp. nov. The type specimen. Slightly reduced.

b. L. indica Hauck. A cotype specimen? in the Thuret herbarium in Paris. × ca. 6/7.



a



b

PLATE 7

L. Okamurai sp. nov. The type specimen.



PLATE 8

a. L. virgata J. Ag. A cotype specimen in the general herbarium in Paris. × ⅓.

b. L. virgata J. Ag. One specimen of Lamouroux under the name of *L. versicolor* Lamx. in the herbarium of Lamouroux. × ca. ⅚.



a



b

PLATE 9

L. nipponica sp. nov. The type specimen. Slightly reduced.



PLATE 10

L. Masonii Setch. et Gard. var. *orientalis* var. nov. The type specimen. $\times 9/10$.


HERB. K. YEN
ucia paniculata

PLATE 11

a. *L. japonica* sp. nov. A cotype specimen, young. Slightly magnified.
b. *L. japonica* sp. nov. The type specimen. × 1.

a



b



PLATE 12

a. L. coronopus J. Ag. The type specimen in the herbarium of J. Agardh. No. 37080. × ca. ½.

b. L. gracilis Hook. et Harv. An authentic specimen in the herbarium of Hooker.



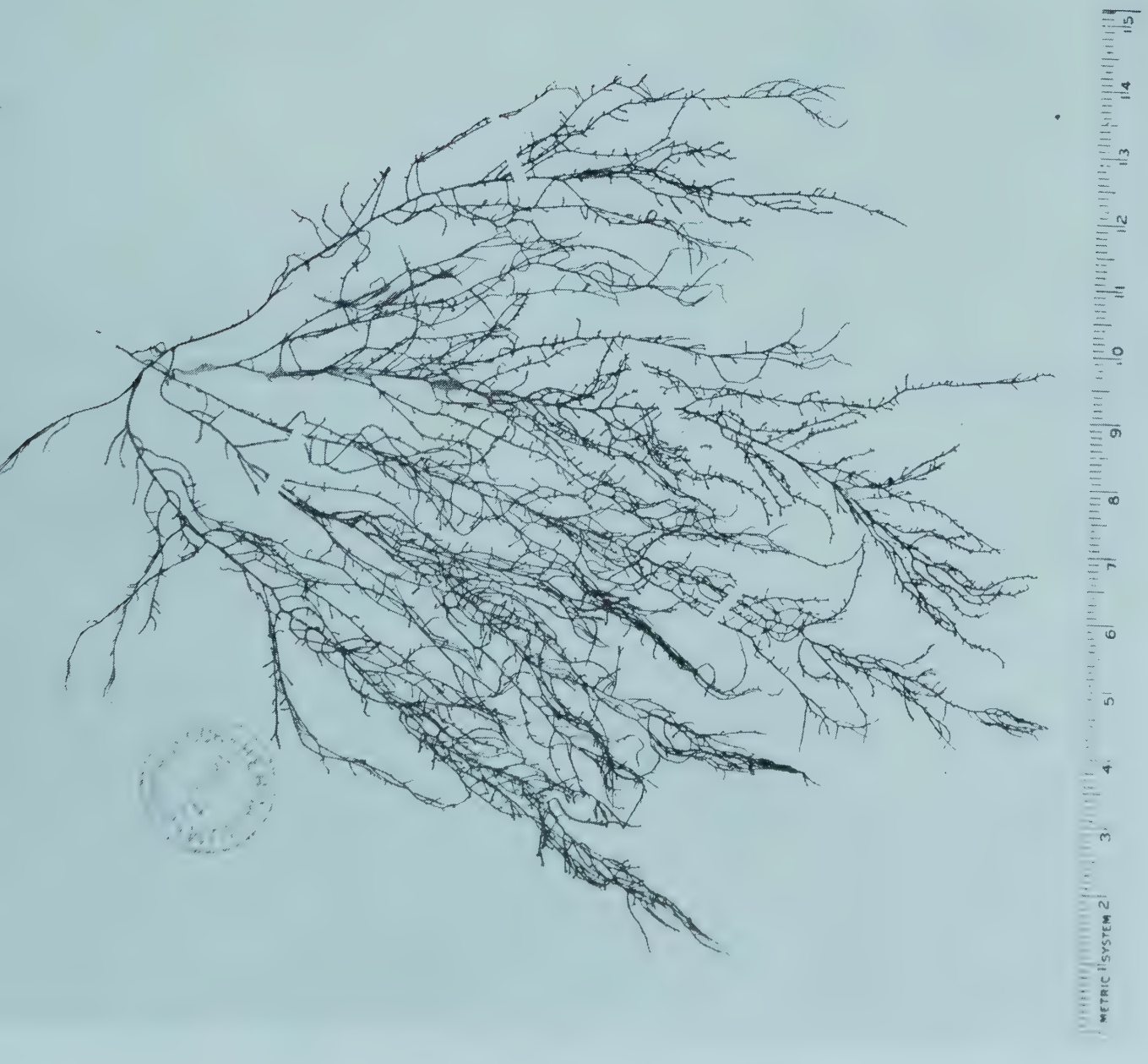
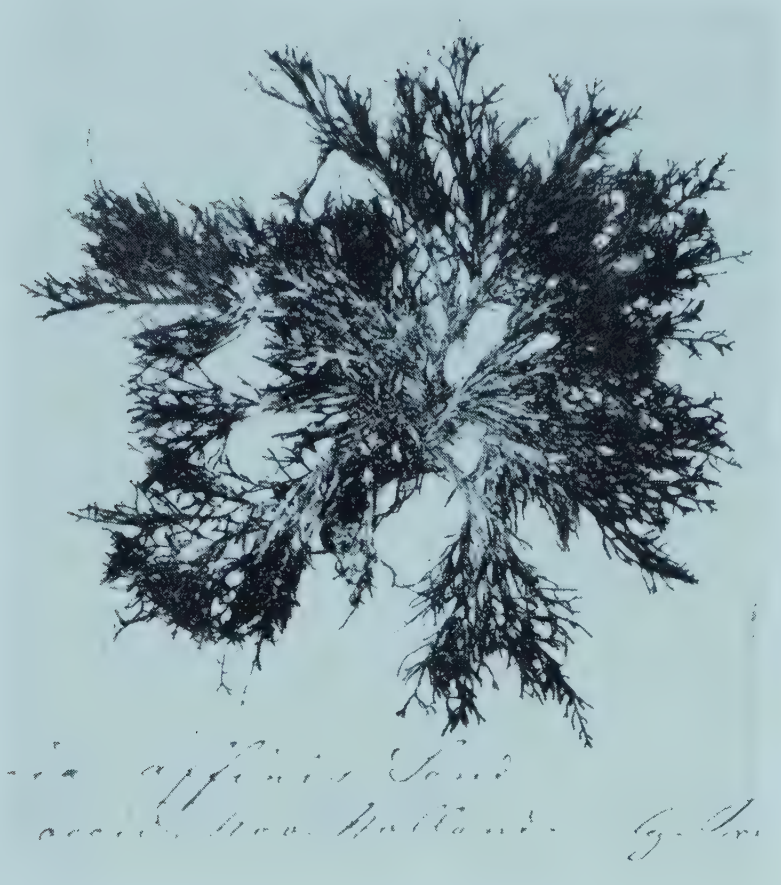

METRIC SYSTEM 2

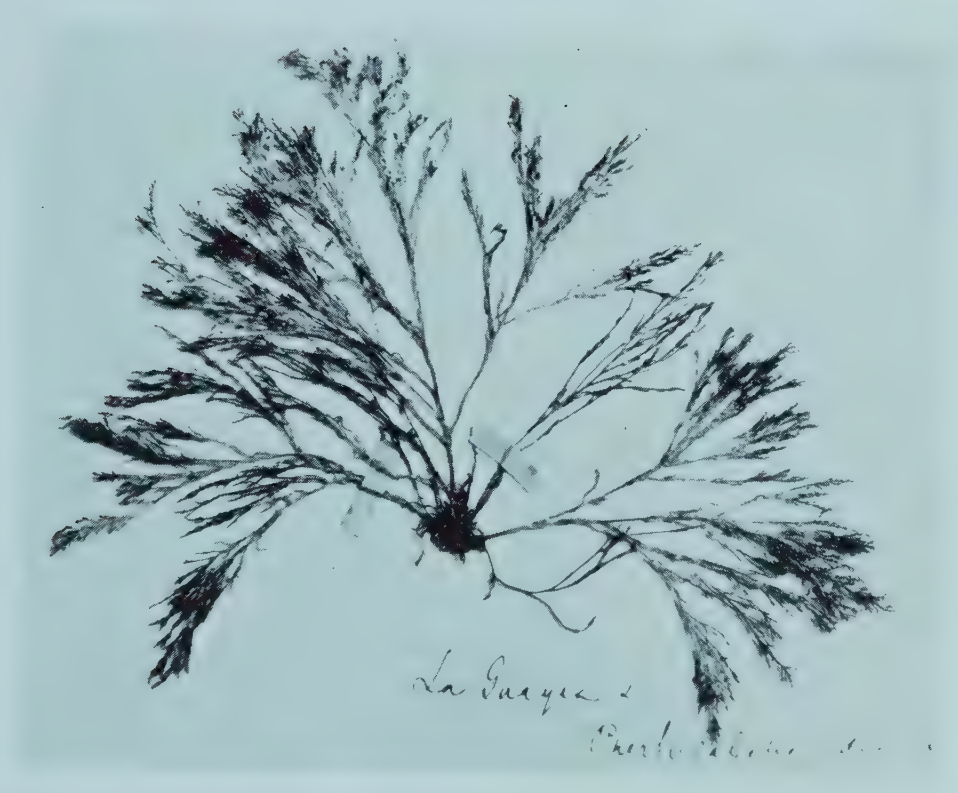
PLATE 13

a. L. Forsteri f. *affinis.* An authentic specimen of *L. affinis* Sond. in the herbarium at Kew. × 1.

b. L. scoparia J. Ag. The type specimen in the herb. of J. Agardh. No. 36610. × ca. 5/8.



a



b

PLATE 14

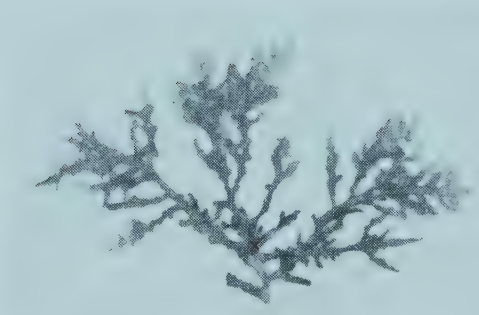
L. capituliformis sp. nov. The type specimen. Slightly reduced.



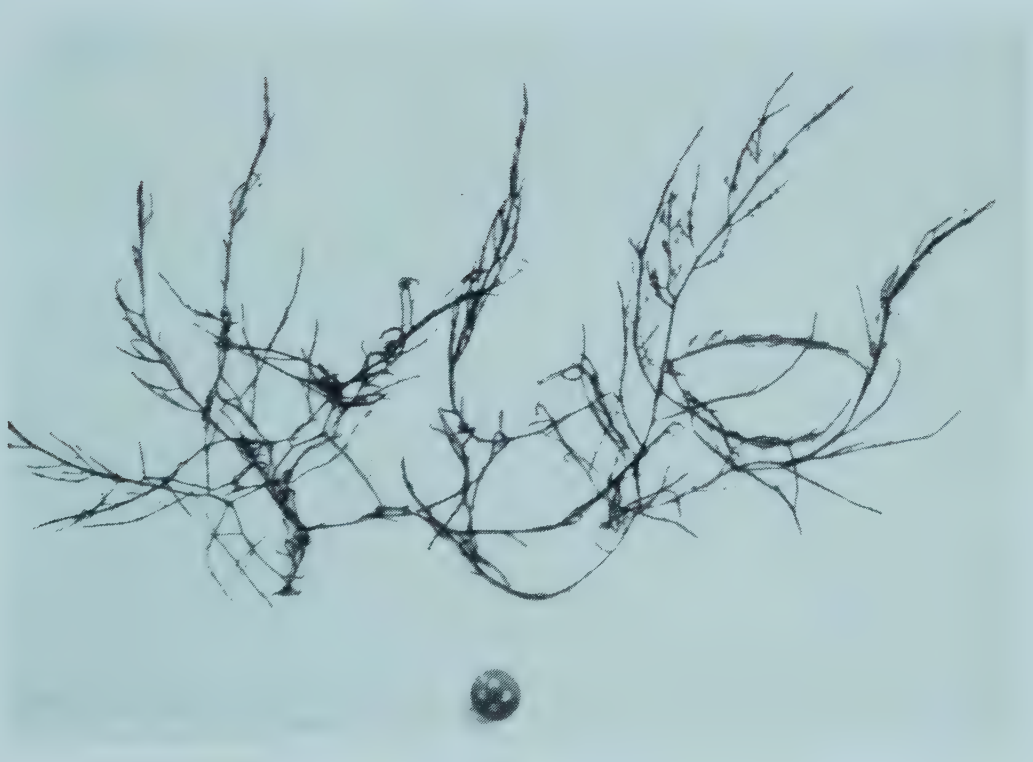
PLATE 15

a. L. Poitei (Lamx.) Howe. The type specimen of *Fucus Poitei* Lamx. in the herbarium of Lamouroux. × ca. 5/6.

b. L. subopposita (J. Ag.) Setchell. The type specimen of *Chondriopsis subopposita* J. Ag. No. 37633 in the herbarium of J. Agardh. × ca. 5/9.



a



b

PLATE 16

a. L. obtusa var. *divaricata.* The type specimen of *L. divaricata* J. Ag. in the herbarium of J. Agardh. No. 36642. × ⅔.

b. L. obtusa var. *Snackeyi.* A specimen from the Palao Islands. × ⅖.

c. L. obtusa var. *majuscula* Harv. An authentic specimen in the herbarium of Harvey. × ca. 8/15.



a



b



c

PLATE 17

a. L. dendroidea J. Ag. The type specimen in the herbarium of J. Agardh. × 12/17.

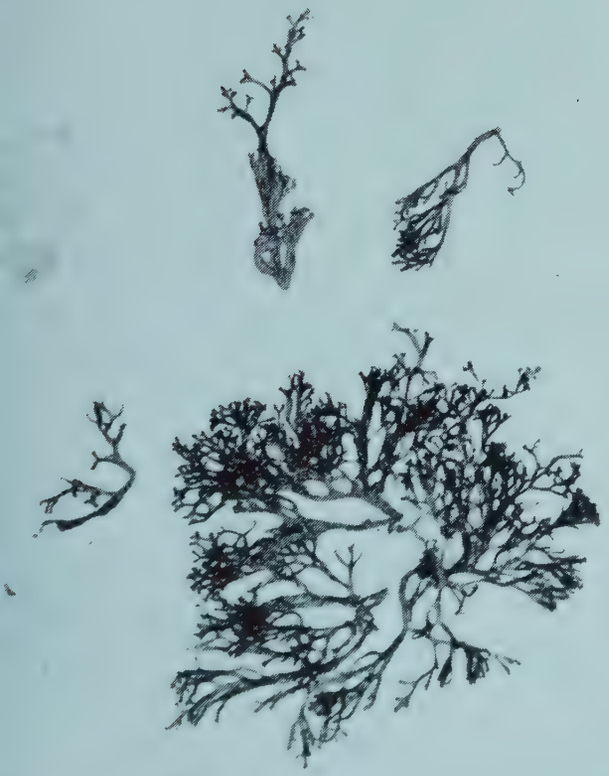
b. L. obtusa var. *intricata.* An authentic specimen of *L. intricata* Lamx. in the general herbarium in Paris. × 7/8.

c. L. obtusa var. *densa.* The type specimen, slightly reduced.



a

Laurencia intricata Lamx.



b

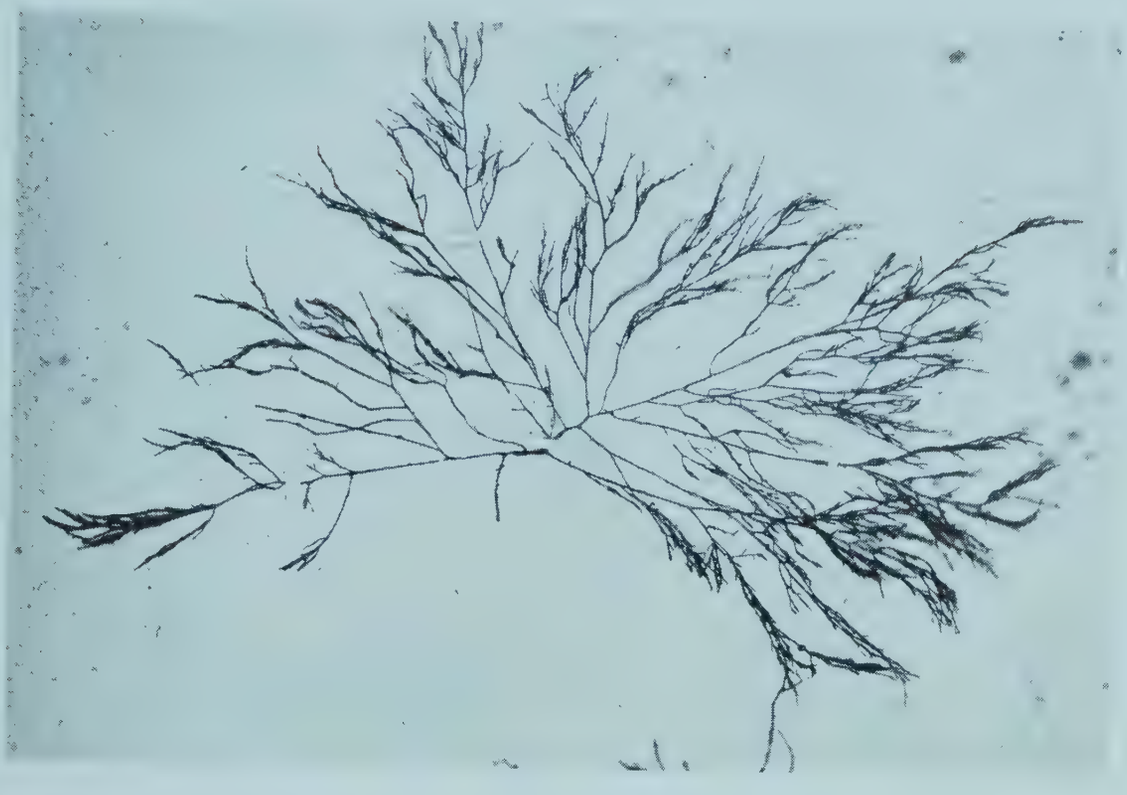


c

PLATE 18

a. L. filiformis Mont. The cotype specimen of *Chondria filiformis* C. Ag. in the general herbarium in Paris. × ca. ½.

b. L. rigida J. Ag. An authentic specimen (the type?) in the herbarium of J. Agardh. No. 36694. × ca. ⅝.



a



b

PLATE 19

a. L. cartilaginea sp. nov. The type specimen. Slightly reduced.

b. L. Casuarina J. Ag. An authentic specimen in the herbarium of J. Agardh. No. 37017. × ca. ⅔.





PLATE 20

L. tropica sp. nov. The type specimen. × 1.



PLATE 21

L. tasmanica Harv. An authentic specimen in the herbarium of Hooker.



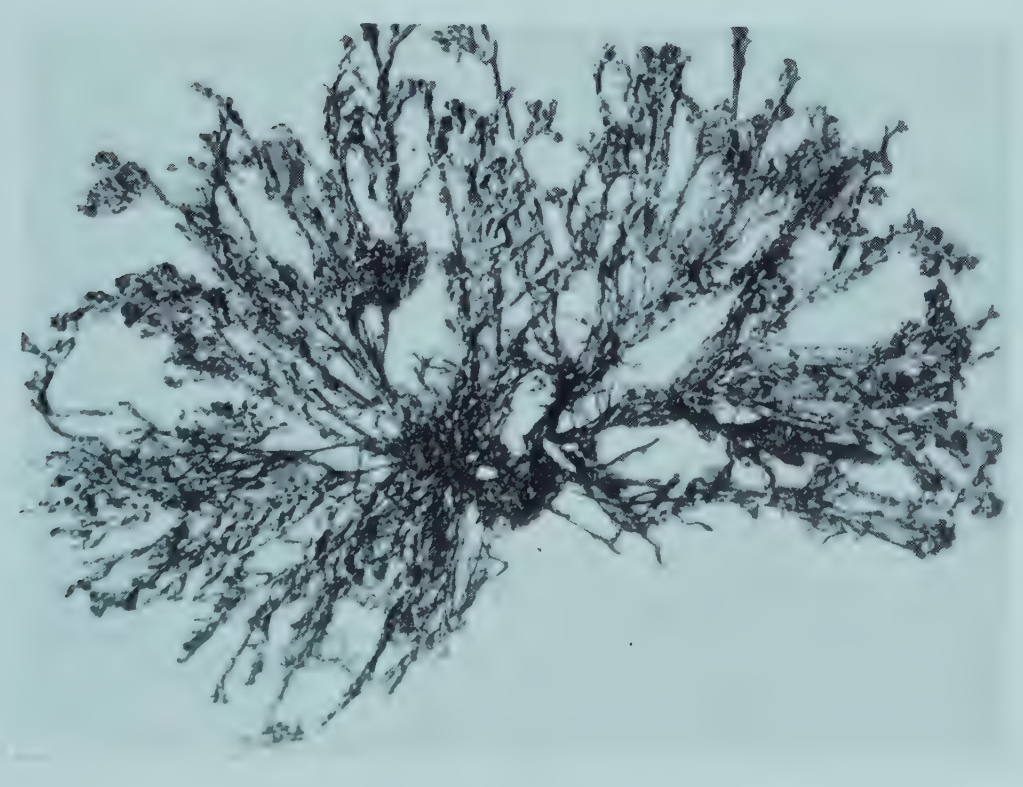
PLATE 22

a. L. regia Harv. Harvey's Austr. Alg. No. 237 in Thuret's herbarium in Paris. × ca. 3/5.

b. L. corymbosa J. Ag. A cotype specimen in the general herbarium in Paris. × 10/17.



a



b

PLATE 23

L. composita sp. nov. The type specimen. × 9/10.



PLATE 24

L. Yendoi sp. nov. The type specimen.



PLATE 25

a. L. Brongniartii J. Ag. A cotype specimen in the general herbarium in Paris. × ca. 2/5.

b. L. Brongniartii J. Ag. The type specimen of *L. concinna* Mont. in the herbarium of Montagne. × 4/5.



a



b

PLATE 26

a. L. elata Harv. The type specimen of *Chondria pinnatifida elata* C. Ag. in the general herbarium in Paris. × ca. ¼.

b. L. elata Harv. One of Harvey's specimens in his herbarium. × 7/18.



a



b

PLATE 27

L. luxurians (Harv.) J. Ag. No. 37245 in the herbarium of J. Agardh. × ca. ½.



PLATE 28

L. pinnata sp. nov. The type specimen. × 1.



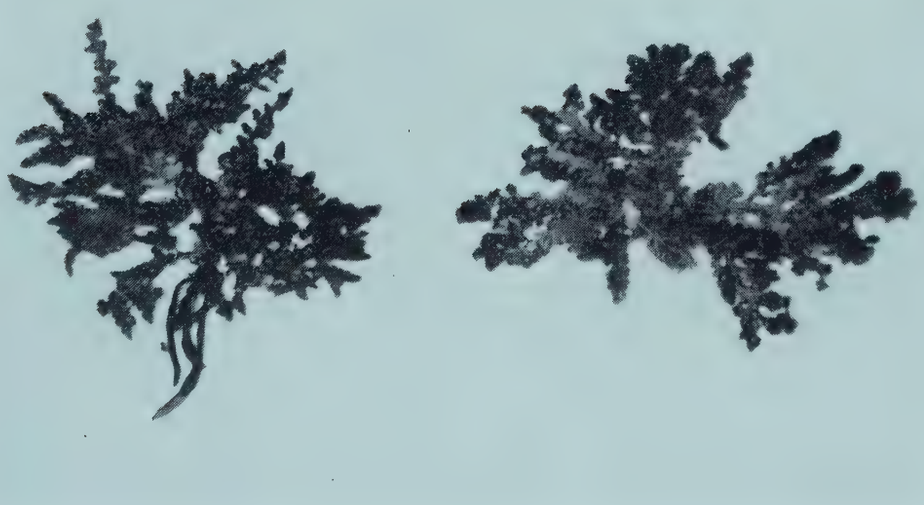
PLATE 29

a. *L. undulata* sp. nov. The type specimen. Slightly magnified.

b. *L. botrychioides* Harv. The authentic specimens (the type?) in the herbarium of Harvey. × 5/6.



a



b

PLATE 30

a. L. ceylanica J. Ag. One specimen in the herbarium of Harvey. Ceylon Alg., No. 17. × 1.

b. L. thyrsifera J. Ag. The type specimen in the herbarium of J. Agardh. No. 36976. × ⅔.



a



b

CHIASMAS IN FLOWERING PLANTS

BY

JOHN BELLING

University of California Publications in Botany
Volume 16, No. 8, pp. 311–338, 11 figures in text
Issued June 2, 1931

University of California Press
Berkeley, California

Cambridge University Press
London, England

CHIASMAS IN FLOWERING PLANTS*

BY

JOHN BELLING

INTRODUCTION

Chiasmas in plants.—Nodes or chiasmas in the bivalents of diploid and triploid *Hyacinthus orientalis* were figured by the writer in 1925; and though the genetic facts pointed to segmental interchange between homologous chromosomes as an accompaniment of chiasmas, yet the cytological evidence did not seem to be sufficient to establish it. In the next year, the writer showed that, in the reduction divisions of *Uvularia grandiflora,* the internodes (V's or rings) separated at early anaphase in the same way as, long before, they had been observed to separate in animals. In 1927, Newton figured nodes and chiasmas of Tulipa in early and late diaphase. In the same year, the present writer decided, from a study of the nodes in the bivalents and trivalents of *Hyacinthus orientalis,* that the working hypothesis of Janssens and Morgan, namely segmental interchange (crossing over), was preferable to the older hypothesis in explaining the chiasmas of plants. An attempt was made to count the average numbers of chiasmas. Apparent terminal junctions (some of which may have been subterminal chiasmas) were not included, and configurations which could not be accurately counted were omitted. Hence the numbers obtained were doubtless somewhat too small. In 1928 the results of the writer's work on the nodes and chiasmas of some species of Lilium appeared. Here the comparison of early, middle, and late diaphase showed a decrease in the number of nodes. Most (but not all) of the nodes at early diaphase were chiasmas, as was shown by observation at early anaphase. The so-called "strepsinema" was not mainly due to twisting, but to the presence of chiasmas. In 1930, Maeda demonstrated that in *Vicia faba* the nodes or chiasmas varied in number from 1 to 6 in the short

* This paper reports the results of cytological work done under the Carnegie Institution of Washington.

bivalents, and from 2 to 13 in the long bivalents; the average numbers being proportional to the lengths of the two kinds of chromosome. Maeda also published a study of the nodes or chiasmas in *Lathyrus odoratus,* showing that they varied from 1 to 7 in a bivalent. In the same year (Newton and) Darlington proved, that in *Fritillaria meleagris,* the nodes, at middle diaphase, were, as a rule, near the primary constriction; the average number found being 2.3 for bivalents with subterminal, and 2 for bivalents with median constrictions. In his paper of 1931, the present writer stated his modification of the Janssens-Morgan hypothesis of crossing over, and showed that it was probable that the primary split alone opens out in plants at diplotene. Darlington (1931) proved that nodes disappear during early and late diaphase in *Primula sinensis.*

Chiasmas in animals.—These were studied at least twenty years before the chiasmas of plants. After the important papers on Batrachoseps by Janssens in 1905 and 1909, and the adoption of his hypothesis by Morgan and his co-workers in genetical work at about 1911, the hypothesis of Janssens was definitely rejected for cytology in 1916, in the excellent papers of both Robertson and Wenrich on the maturation divisions of certain grasshoppers. The authority of these two papers seems to have ruled most cytologists for ten years or more. Meanwhile Gelei's masterly account of the early stages of maturation in the ova of Dendrocoelum showed that the secondary split appeared during the pachytene stage, and that it was throughout subsidiary to the primary split, which latter seemed to open out alone at diplotene. The final voluminous paper of Janssens, which appeared in 1924, did not decide the question at issue. In 1924, Morgan published an excellent account of the chiasma-crossing-over hypothesis as applied in genetic work. In fact, our knowledge of the chromosomes which is due to the workers who have dealt with the genetics of *Drosophila melanogaster* seems to the writer to have equaled, and in some ways surpassed, what the workers with the microscope have been able to find in the chromosomes of other animals, or of plants. Hence any valid hypothesis as to chiasmas and crossing over should satisfy both the genetic facts, and also the phenomena seen with the microscope.

THE TWO HYPOTHESES

The first hypothesis.—This hypothesis did not take account of crossing over. It considered a chiasma as the result of openings out, on the one side between homologous chromatids, and on the other, between sister chromatids. These openings out were presumed to occur in a uniform pachytene thread having two equal splits at right angles. The internodes were supposed to be, alternately, combined sister strands and combined non-sister strands. However, one such opening out having occurred, the next opening out, on either side of it, would have, in the writer's opinion, an equal chance to be the same as the first, or to be different. Then there would not be a regular alternation of opposite openings out at early diplotene. Also, since the two sister strands seem always to keep together at the primary constriction, if the nearest chiasma separated sister strands on the side of the chiasma toward the primary constriction, as would happen by chance in half of the cases, then there would also be a double cross-junction formed at the constriction. Hence this hypothesis is not so simple as it might appear at first.

The second hypothesis.—This hypothesis applies both to chiasmas and to crossing over. It postulates that segmental interchange between homologous chromosomes accompanies the formation of chiasmas. It is based on half-twists of the two synapsed chromosomes. In the writer's modified form (1931) the newly formed chromioles, at the time of cleavage or just before, are supposed to make their longitudinal junctions *the shortest way* lengthwise. This produces crossing over, without breaks occurring in the chromosomes.

The hypotheses contrasted.—(1) The first hypothesis, in its simple form, fails to account for any chiasmas which may be connected with crossing over. Crossing over has been proved to be of widespread occurrence. In Matsuura's careful account (1929) of the genetic work on plants from 1900 to 1925, there are about thirty genera named in which crossing over has been fairly well or thoroughly proved. Also the number of chiasmas observed in Lilium at late diaphase and metaphase has been shown by the writer to be not much different from the number necessary to account for the crossing over in the long chromosomes of Drosophila. Here, then, there may be no

chiasmas left to be accounted for by any hypothesis of alternate openings out.

(2) The first hypothesis appears to fail with unequal homologues that have one or two chiasmas, and the primary constriction near one end (fig. 1). For, on this hypothesis, in about half the cases, the unequal limbs of the distal open internode should have opened at *diplotene* between sister strands. This has not been observed. On the second hypothesis, no such opening out between sister strands should occur.

(3) On the first hypothesis, in a bivalent with unequal homologues, these should always separate at *anaphase* into short and long homologues. But in some cases they are observed to separate into

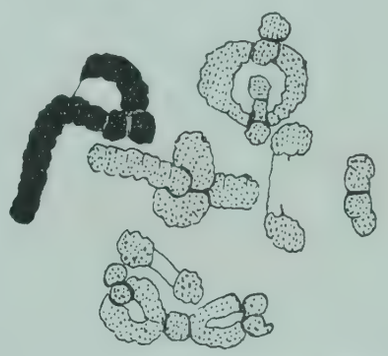


Fig. 1. Camera drawing of iron-acetocarmine preparation of pollen-mother-cell of *Aloë purpurascens*. This particular plant had, in all cells examined, one bivalent with unequal homologues, which is in solid black in the figure. It has here apparently only one chiasma, while the three other long bivalents have more than one chiasma each. One of the three short bivalents shows a broken connecting thread and an unbroken one. Drawn at table level, with the 70 apochromatic water-immersion objective, and the 15-times compensating eyepiece.

short plus long and short plus long chromatids. This is expected on the second hypothesis.

(4) The first hypothesis is more or less connected with the hypothesis of extensive sliding of the chromatids along one another *during diaphase*. But this is mostly hindered by the zigzags of the chromonemas. It is possible that an apparent effect of having moved was produced by the different positions of the chiasma or chiasmas in the same bivalent in different cells. This difference of position is now known to occur normally. (Newton and) Darlington (1930) found that such sliding did not occur in *Fritillaria meleagris*, where it had been at first postulated. Of course, sliding of chiasmas occurs in early anaphase; and it may also occur at early diplotene.

(5) The first hypothesis appears not to agree with the observations of Gelei (1921) and of the writer (1930), that the primary split alone opens out at diplotene.

(6) The first hypothesis seems to the writer to fail with trivalent configurations showing two chiasmas with different homologues, on the same side of the primary constriction. In this case there are certain internode halves in which, on the first hypothesis, both sister strands and homologues should open out at once; and this appears to invalidate the first hypothesis. As the writer has shown (1929), trivalents are readily explained by the second hypothesis. The same applies to quadrivalents (Darlington, 1930).

(7) On the first hypothesis, it seems that the alternate internodes should be at right angles from the first. On the second hypothesis,

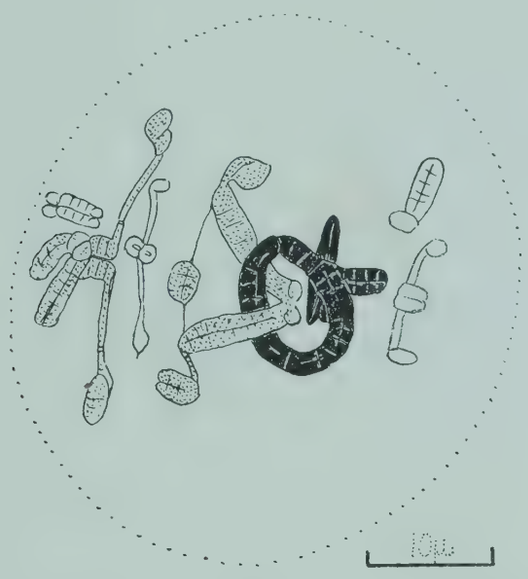


Fig. 2. Camera drawing of a preparation of *Uvularia grandiflora* in iron-acetocarmine, showing two bivalents interlocked. (Similar interlocking has been previously figured by Robertson, Gelei, and others.) It is obvious that both interlinked openings out must be at the primary split.

they should be nearly in one plane at first, and at right angles only after shortening. The latter appears to be the case.

(8) On the first hypothesis, two bivalents at diaphase or metaphase interlocked like two links of a chain (fig. 2) should in about half the cases show opening out between sister chromatids. This interlocking must have occurred before any opening out (since it happened at synapsis). In this case it is easy to distinguish between the two kinds of opening out. The known cases of interlocking seem to show opening out only between homologues, as required by the second hypothesis.

(9) If the secondary split, as the first hypothesis requires, opens out at diplotene as much as the primary split; then when the primary split is no longer present, as in haploid plants, one might expect to find some trace of the opening out of the secondary split at diaphase.

This does not seem to occur. On the second hypothesis it need not occur.

(10) A hypothesis to explain chiasmas would be more useful if it also explained deficiency, translocation, reciprocal translocation, and inversion. The first hypothesis does not offer to explain these. The writer's modified form of the second hypothesis can explain them without difficulty.

(11) The openings out at diplotene seem to occur at a greater number of places than would be required on the first hypothesis, even when allowance is made for consecutive openings out of the same kind. On the second hypothesis, it matters not how many temporary points of opening out are formed at early diplotene.

(12) Since, on the first hypothesis, chiasmas are not connected with crossing over, they might well appear in animals that had no crossing over, such as the male Drosophila; and they might well be absent in animals or plants in which crossing over had been demonstrated, such as *Lathyrus odoratus*. The evidence on this point is still meager, but so far it seems to agree best with the second hypothesis.

(13) A good test of a working hypothesis is its use in the work of prediction. The first hypothesis has lately been tested as a means of prediction by (Newton and) Darlington, and has not succeeded (Darlington, 1930). The second hypothesis has long been used for prediction by Morgan and his co-workers, and has succeeded so far.

The first hypothesis (alternate openings out), combined with subsequent breakage at the X of the chiasma, as advocated by Sax (1930), still seems to the writer to be counter to Nos. 2, 5, 6, 7, 8, 9, 10, and 11 above.

An objection to the writer's hypothesis of crossing over (which is described below) is that it does not account for chiasmas unaccompanied by crossing over, which are supposed to occur in some male grasshoppers. But proof of the absence of crossing over here seems still wanting.

THE WRITER'S HYPOTHESIS OF CROSSING OVER

This hypothesis, which has been briefly described in a previous paper (1931), assumes that half-twists occur in the paired homologues at early pachytene, before the secondary split has begun. The secondary split comes at late pachytene, after the twist is established. Figure 3 is a diagram of a chiasma, according to this hypothesis. It is

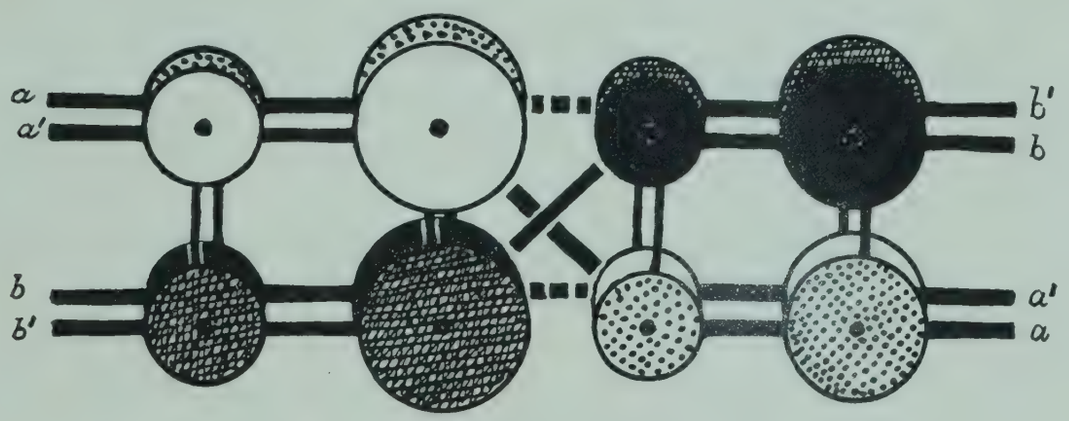


Fig. 3. Diagram to illustrate the writer's modified hypothesis of crossing-over at a half-twist.

assumed that the resulting chromioles form new connecting threads, or take up the old connections, in all cases by the shortest path. That is, when a chromomere is cleaving to form two chromioles, the old connecting fiber is indifferent as to which chromiole it will remain with, and this is to be determined by the rule of the short route; and where routes are equal, by chance. At the chiasma the chromioles will be drawn together longitudinally by the twist, and the distance between them will be relatively shorter than in figure 3. The new longitudinal threads will pass straight (either above or below) as shown by the dotted lines. The threads of the X will be taken up by four chromioles on the same level (either below or above), since these are nearer together than those on different levels. Hence there will be, at every such chiasma, two crossovers between homologues, and two crossovers between sister strands. In figure 3, if the attachment constriction is on the right, then the left-hand part has undergone a half-twist at the chiasma. Consequently strand b′ on the right will join on at the chiasma with either a or b on the left, giving two kinds of chiasmas. Suppose b′ on the right joins on with a on the left. Then

a′ on the right will join with b on the left; while b and a on the right will be connected through the X with b′ and a′ on the left respectively. In this case the X is supposed to be above; but, if it is below, the genetic crossovers ba′ and ab′ will result, and the crossing over sister strands will be b′b and a′a.

A second chiasma from the attachment constriction will also be of one of two kinds. Thus there will be four kinds of double chiasmas. The result will be, on the average, four strands with no genetic crossing over (the double crossing over of sister strands having cancelled out), eight strands with single genetic crossing over which takes the form of ab or a′b′ (because of single crossing over between sister strands), and lastly four cases of double genetic crossing over of the form b′a + ab′ or ba′ + a′b. In all there will be 16 genetic crossing over points, of which 8 will have the form ab′ or a′b, while the other 8 will have the form ab or a′b′.

If we follow a third chiasma we shall get 4 strands with no genetic crossing over (but with crossing over between sister strands which has not cancelled out), 12 strands with single crossovers of the form ab or a′b′, 12 strands with double crossovers apparently of the form ab or a′b′ plus the form a′b or ab′, and 4 triple crossovers of the a′b or ab′ form. Hence there will be 48 points of genetic crossing over, of which 24 will be of the ab or a′b′ form, and 24 of the a′b or ab′ form.

If two adjacent chiasmas are both of the form ab or a′b′, or both of the form a′b or ab′, they may be called direct double chiasmas. But if one is of the form ab or a′b′ and the other is of the form a′b or ab′, then they may be called oblique double chiasmas. By the writer's hypothesis, because of the crossing over between sister strands, the double or triple chiasmas will be of the direct form, and the crossing over between a and b or a′ and b′ will be of equal frequency with the crossing over between a and b′ or a′ and b.

The above hypothesis of half twists leading to the formation of new connections agrees with the following facts. Anderson (1925), in his important study of the crossing over in Drosophilas with attached X's, proved (the chromatids being ab and a′b′) that a crosses over with b as frequently as with b′, and also that a′ crosses over equally often with b and b′. The writer's hypothesis given above agrees with this. The writer examined two bivalents of *Lilium candidum* with double chiasmas in which, by a rare chance, the four strands could be

accurately followed. To these two cases were added eleven drawings of double chiasmas from papers by Robertson, Wenrich, Janssens, and Granata, mostly on grasshoppers. All these 13 cases showed direct, not oblique, double chiasmas, in agreement with the writer's hypothesis.

Crossing over may also occur, on the writer's hypothesis, between two chromosomes which overlap without twist. If they were synapsed chromosomes, genetic crossing over would occur only between a and b or a′ and b′. There would be no crossing over between sister strands. Such overlapping might well happen at the attachment constriction. This is perhaps the cause of the formation of the double half chromosome of the secondary mutants of *Datura stramonium*. Overlapping of non-homologous chromosomes about to begin division might well lead to segmental interchange between them. Overlapping in a loop of a single chromosome about to divide might lead to inversion, or to a large deficiency.

The bar gene of Drosophila is perhaps a new gene, not having passed the ordeal of selection. Hence it might form a very small chromomere, and the two small chromioles might pass to the same strand when a crossover occurs next them, one connecting fiber passing them by. Since crossing over between sister strands happens, on the writer's hypothesis, only between the two strands which do not cross over genetically, such crossing over between sister strands would have no effect on the genetic results with bar.

CHIASMAS AND CROSSING OVER

Number of chiasmas.—On the writer's hypothesis it will perhaps be possible to calculate the amount of genetic crossing over from the number of chiasmas, and vice versa.

One bivalent with no chiasma yields $4n$ chromatids
..... with 1 chiasma yields $2n + 2s$ chromatids
..... with 2 chiasmas yields $n + 2s + d$ chromatids
..... with 3 chiasmas yields $\frac{n + 3s + 3d + t}{2}$ chromatids
..... with 4 chiasmas yields $\frac{n + 4s + 6d + 4t + q}{4}$ chromatids

where $n =$ non-crossover, $s =$ single crossover, and so on. Thus if a is the number of bivalents with no chiasmas, b is the number with one chiasma, and so on; then on the average, the number of

$$\text{non-crossovers} = 4a + 2b + c + \frac{d}{2} + \frac{e}{4}$$

$$\text{single crossovers} = 2b + 2c + \frac{3d}{2} + e$$

$$\text{double crossovers} = c + \frac{3d}{2} + \frac{3e}{2}$$

$$\text{triple crossovers} = \frac{d}{2} + e$$

$$\text{quadruple crossovers} = \frac{e}{4}$$

It is easy to count the permanent chiasmas in Lilium at late diaphase, when there are no temporary nodes. (Since late diaphase is unclear in Hyacinthus, metaphase counts of chiasmas remain doubtful in this plant.) But there is a difficulty with the terminal junctions. Some of these are obviously not chiasmas, since they consist of a very thin thread, and the chromatids at this stage are thick. That some of such terminal junctions were chiasmas at an earlier stage has been made probable in Primula (Darlington, 1931). There is a gradation between these terminal junctions and others which may be subterminal chiasmas merged in the thickening of the bivalent. Since these two kinds cannot be clearly distinguished, it has seemed best at first to calculate both with and without terminal junctions.

Nine cells at late diaphase or metaphase (7 from *Lilium longiflorum,* 1 from *L. regale,* and 1 from *L. speciosum*) showed all 12 bivalents clearly. When the terminal junctions were omitted, these showed in percentages:

25 bivalents with 1 chiasma
47 bivalents with 2 chiasmas
22 bivalents with 3 chiasmas
5.5 bivalents with 4 chiasmas.

When these were calculated, they gave, in percentages:

27 chromatids with no crossovers
46 chromatids with one crossover
22 chromatids with two crossovers
4 chromatids with three crossovers
0.3 chromatid with four crossovers.

With all terminal junctions counted in, there were:

10 bivalents with 1 chiasma
44.5 bivalents with 2 chiasmas
34 bivalents with 3 chiasmas
10 bivalents with 4 chiasmas
1 bivalent with 5 chiasmas.

According to the assumptions used here, these should yield:

21 chromatids with no crossovers
43 chromatids with one crossover
28 chromatids with two crossovers
7 chromatids with three crossovers
1 chromatid with four crossovers
0.03 chromatid with five crossovers.

Hence the inclusion of all apparently terminal junctions does not make a radical difference in the crossing-over numbers, and they will be included in future calculations.

For the inverse calculation we have the percentages of crossover chromosomes given by Morgan (1926) for the first chromosome of *Drosophila melanogaster*. This chromosome resembles most of the chromosomes of Lilium in having a terminal (or subterminal) attachment constriction. These figures were:

43.5 chromosomes with no crossing-over points
43 chromosomes with one crossing-over point
13 chromosomes with two crossing-over points
0.5 chromosome with three crossing-over points.

This shows an excess of chromosomes with no crossing over. But, by the calculation, the chromosomes with one crossing over should be in excess. The excess of non-crossovers may be due to loss of some instances of single crossing over at the ends of the chromosome, and this seems not unlikely. Or it may perhaps be due to some bivalents having no crossing over, and being attached by true terminal junctions, not by chiasmas; as is the case perhaps in the male Drosophila.

A calculation as if the data were complete, and to include bivalents with no chiasmas, gives in percentages:

12 bivalents with no chiasmas
37 bivalents with one chiasma
46 bivalents with two chiasmas
4 bivalents with three chiasmas.

(But if we assume that the bivalents calculated as having no chiasmas had each a chiasma causing a crossing over which was not found, there would be nearly equal numbers with one and with two chiasmas.) This shows that the X chromosome (assuming that experimental errors are negligible) has many more no-chiasma bivalents and more single-chiasma bivalents than Lilium, about the same number with two chiasmas, and many fewer with three chiasmas. No-chiasma bivalents have been seen by the writer in Tulipa and Hyacinthus. From the

nature of the attraction between the chromosomes of Diptera, and the possible absence of chiasmas in the male Drosophila, such no-chiasma bivalents seem not unlikely to occur also sometimes in the female Drosophila, if the assumptions underlying these calculations prove to be correct.

Positions of chiasmas.—The two longer bivalents of Lilium have attachment constrictions intermediate between terminal and median. The other ten bivalents have attachments varying from subterminal to terminal. We will consider the positions of the chiasmas nearest the ends. If these chiasmas are in random positions, and if one-quarter or more of the mean length of the internodes is counted as long (L), and less than one-quarter as short (S), for the free ends; then by chance there might be expected 3L to 1S among these free ends. But at the late diaphase of Lilium, observation gave 9L to 11S for the two long bivalents, and 43L to 57S for the ten bivalents with nearly terminal attachment constrictions. Since the end junction of the leptotene threads, at the start of the zygotene stage, proceeds, in known cases (Gelei, 1921; Wenrich, 1916; Janssens, 1924; Belar, 1929) by approximation of the distal ends, and perhaps also follows this method in the bivalents of Lilium with subterminal attachment constrictions, there might well be a first chiasma not far from the distal end. The next chiasma would usually be at a distance of about the usual modal internode length, and so on, leaving at the proximal end (in the ten shorter bivalents) a free length determined by chance. If this is the case, there might well be an excess of short free ends, especially at the distal ends of the bivalents. The free ends were measured in a cell which showed all twelve bivalents clearly at early diaphase, and was pressed flat. The eleven long free ends (measuring from 6 to 18 units) averaged 9.5 units; while the thirteen short free ends (from 1 to 4 scale units in length) averaged 2.2 units. (However, in another cell at the same stage, not adapted for measuring, there were more long free ends.) The metaphase of Lilium shows that the ten shorter bivalents usually have long ends where the attachments of the spindle fibers are seen. Examination of three metaphase cells in which all twelve bivalents were clear, gave, at the distal ends, fourteen long free ends to twenty-eight short ones; while the ends with the attachments fibers were mostly long.

Crossover charts.—Eighteen long bivalents of Lilium, in nine cells, at late diaphase and at metaphase, had an average of 3.7 chiasmas each; while the ninety bivalents with terminal or subterminal attach-

ment constrictions, in the same cells, had an average of 2.2 chiasmas. In the latter kind of bivalent, the first chiasma from the distal end would often be, as shown by measurement, less than a quarter of the modal internode length from that end. Thus there would be a space at the distal end of each of these chromosomes where crossing over would be rare, followed directly by a space where crossing over is abundant. This might be followed, at a distance equal to the modal internode length, by another space where crossing over is also relatively abundant. In a crossover chart, this would be shown by a close crowding of the genes at the distal end, followed by a region of widely spaced genes; with indications of a second widely spaced spot, an internode away from the first. The first chromosome of *Drosophila melanogaster* appears to agree with this in its crossover chart, when allowance is made for its having fewer chiasmas than the short chromosomes of Lilium, its average being perhaps about 1.5 to a bivalent. The second chromosome of *D. melanogaster* seems to resemble the short chromosomes of Lilium in *each* of its two limbs (Dobzhansky, 1930); but the third chromosome does not appear to conform to this scheme (Dobzhansky, 1929), having only weak or no crowding at the ends.

Lengths of internodes.—The lengths of the internodes can be best measured in a flattened cell at early diaphase. Allowance must however be made for the fact that nearly a third of the nodes at this stage are perhaps not chiasmas. In such measurements it is, in the writer's opinion, preferable to flatten the bivalents by just sufficient pressure, than to try to calculate the lengths for different obliquities. The lengths of these 31 internodes (omitting the free ends) were, in scale units:

Lengths.....	9 to 12	13 to 16	17 to 20	21 to 24	25 to 28
Internodes.....	9	13	4	4	1

The minimum was 9; the average, 15; and the maximum, 28 units. There is here a concentration nearer the minimum, which is to be expected if consecutive half-twists at zygotene tend to keep more or less apart. (At zygotene, when these half-twists occur, the bivalents are, in Lilium, about four times as long as at early diaphase.) Thus the distances between successive chiasmas show some agreement with what might be expected if they are the cause of the distances between

successive crossovers, as shown in the fact of "interference" in Drosophila, and in Primula (Altenburg, 1921).

Opening out of chiasmas.—Chiasmas hold only because the secondary split has not yet opened out. This opening out happens at early anaphase, in Lilium and in other plants showing chiasmas at metaphase. But it seems probable that such opening out may occur at diplotene with short chromosomes which regularly show no chiasmas at metaphase, such as those of Datura or Canna. In any such opening out there may be four kinds of double chiasmas (or sixteen, if we regard direction of twist). When the opening out spreads from the attachment point, two chiasmas which are both on the same side of it will meet. In many of the cases they will both disappear, and in many other cases there will be interlacing between strands, which will require to be pulled apart to the end of the bivalent (as the writer has seen happen in Hyacinthus, Uvularia, and Lilium). Hence with short chromosomes, if the opening out occurs at diplotene, the ends of the chromosomes may remain throughout diaphase connected only by terminal junctions. In cases where no chiasmas are formed, and there is presumably no crossing over, the chromosomes may also be connected by terminal junctions, as in the male *Alydus calcaratus* (Reuter, 1930), and perhaps also in the male Drosophila.

Terminal junctions of bivalents.—Some true terminal junctions may be seen in all plants studied by the writer. (They were also seen occasionally in the diaphase of the grasshopper Chortophaga, and abundantly in Apotettix.) Sometimes all, or nearly all, the junctions at diaphase and metaphase are terminal; as in *Datura stramonium* and *Canna flaccida.* Sometimes only a small fraction of the junctions are terminal, and the rest chiasmas; as in Lilium, Tulipa, and Hyacinthus. Thus in ten selected cells of Lilium, with 120 clear bivalents, there were no less than 29 terminal junctions where the homologues were connected by a short thin thread. It was obvious that these were not chiasmas, since the chromatids were fairly thick at this stage. Thus 12 per cent of the ends of the bivalents had true terminal junctions, not chiasmas. (A number of other end junctions in these bivalents might either have been true terminal junctions or subterminal chiasmas.) Such terminal junctions were clearly seen in *Scilla peruviana,* in early diaphase (fig. 4). If there have been subterminal chiasmas at these end junctions at early diplotene (as is not improbable), they have opened out and vanished, leaving the ends connected only by fine fibers, which (in the writer's opinion) are not

gene strings. But these terminal junctions may sometimes have nothing to do with chiasmas, for terminal junctions between chromosomes may be found where there have been no chiasmas. Thus in the male Alydus, as figured by Reuter (1930), there appear to be no chiasmas at any stage; but there are terminal junctions of the two chromatids of the homologues. Also, in Drosophila, there is found a lasting terminal attachment of two X chromosomes, and an attachment of the

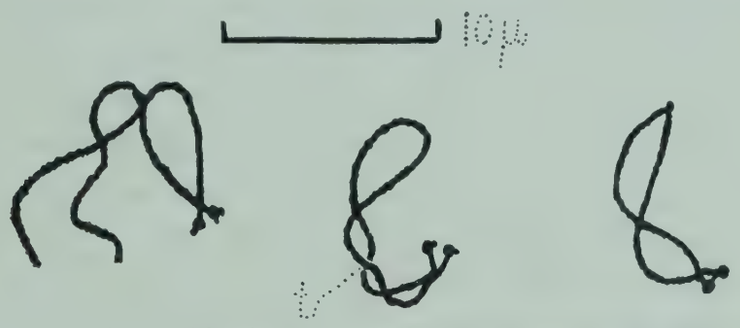


Fig. 4. Three of the bivalents at early diaphase from pollen-mother-cells of *Scilla peruviana*. All three show knobs at one end. The middle bivalent shows a true terminal junction at the upper end, and the right-hand bivalent shows a terminal junction with a small knob. All the nodes are apparently chiasmas or adhesions, except the one marked *t*, which is an overlapping. From a smear preparation fixed with chromic-acetic-formalin, stained with iron-brazilin, and mounted in immersion oil.

X to part of the Y chromosome, as well as a part of the third chromosome with the fourth; in Datura there are terminal attachments of parts of chromosome 9 with chromosome 1; and in Orthoptera there are well marked cases of lasting terminal attachment in multiple chromosomes. In every crossing over there are terminal attachments between the parts of the two crossover chromatids. Of plants which

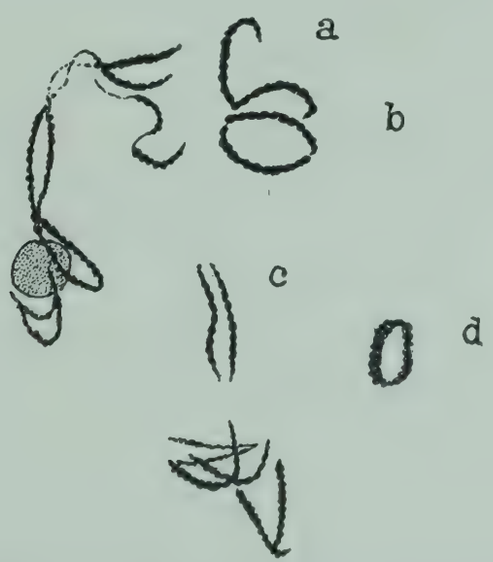


Fig. 5. Camera drawing of a coverglass preparation in iron-acetocarmine of a pollen-mother-cell, at early diaphase, of *Datura stramonium*. Drawn under apochromatic objective 120, with compensating eyepiece No. 8, and 160 mm. tube-length, at table level. The eleven bivalents are clear (*d* being probably a quadrivalent, since this was a $2n + 2$ plant). There are no chiasmas.

have been studied in this respect, terminal attachments are well seen in *Datura stramonium.* Here, with a few exceptional bivalents, the late diaphase and the metaphase show no chiasmas, but end junctions are almost always present. At early diaphase (fig. 5) it is seen that the homologues are usually separated from one another, so that any chiasmas that might have been present previously are as much pulled open as the chiasmas of Lilium are at late anaphase. The ends however are still mostly connected by fine fibers, though these fibers are not always visible, but appear more clearly at middle diaphase (fig. 6), or late diaphase (fig. 7). A case of crossing over is stated to have been found in chromosome 9 of Datura (Blakeslee *et al.,* 1927); so apparently chiasmas must have occurred at diplotene at least in bivalent 9. *Lycopersicum esculentum* seems to resemble Datura in the usual absence of chiasmas at diaphase and metaphase, and the presence of some cases of crossing over. On the other hand, in *Lathyrus odoratus* and *Pisum sativum* crossing over has been thoroughly proved, along with the presence of chiasmas at metaphase.

The writer has observed many chiasmas and a few true terminal junctions in Lilium, Agapanthus, Kniphofia, Tulipa, Fritillaria, Secale, and *Iris versicolor;* and in the long chromosomes of Scilla, Hyacinthus, Aloë, Galtonia, Hosta, Uvularia, and *Hemerocallis fulva.* But no unmistakable chiasmas have been seen yet, by the writer, in *Datura stramonium,* Oenothera, Rhoeo, or *Tradescantia virginiana;* though short straight portions of the chromosomes have been observed to synapse, at a stage equivalent to pachytene, chromomere to chromomere, in Rhoeo. (These were the ends of the chromosomes, and thus the writer's hypothesis of segmental interchange at chromosome ends for Rhoeo and Oenothera is partly confirmed.)

Hence we may apparently assume that, though in many plants with long chromosomes the opening out of the chiasmas is delayed till anaphase; yet, in some plants with short chromosomes, the opening out of the chiasmas may perhaps take place at the diplotene stage. In some plants with both short and long chromosomes, such as Hosta, apparently the short chromosomes open out at diplotene, and the long chromosomes at anaphase. Perhaps, even in Lilium, some opening out, especially of subterminal chiasmas, may take place at diplotene, causing the true terminal junctions observed afterwards. (In plants which presumably open out their chiasmas at diplotene, if the thin threads connecting the chromosomes into bivalents, trivalents, etc., are not well fixed and stained, the observer may assume that an auto-



Fig. 6. Camera drawing of a coverglass preparation in iron-acetocarmine of a pollen-mother-cell, at middle diaphase, of a true tetraploid of *Datura stramonium*. Drawn with the 120 apochromatic objective, and compensating eyepiece No. 12. Threads can be seen connecting the homologues. Some quadrivalents, like L, may have been in quadruple synapsis. There are no chiasmas, only terminal junctions.

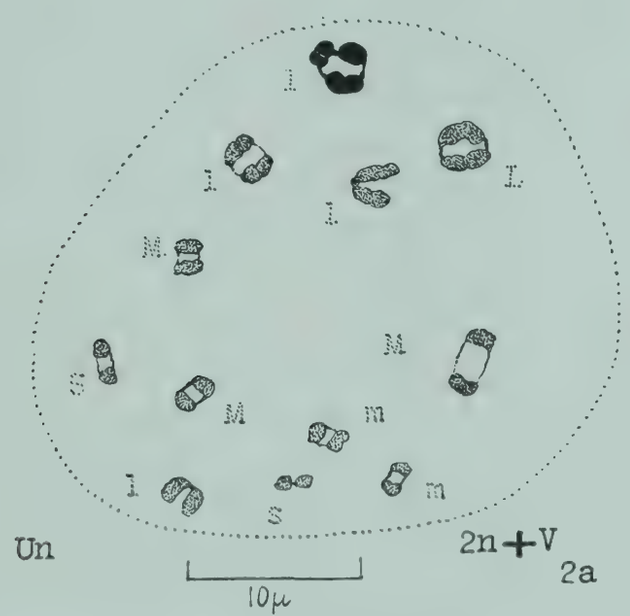


Fig. 7. Camera drawing of coverglass preparation of a pollen-mother-cell, at late diaphase, of *Datura stramonium*, in iron-acetocarmine. This was a secondary mutant having an extra chromosome made of a doubled half of chromosome 5. Two of the eleven bivalents show only one terminal junction. There are no chiasmas.

triploid, for example, may consist of bivalents and univalents, instead of trivalents.) Thus, in the writer's opinion, the presence of terminal junctions is compatible either with the previous presence of chiasmas and crossing over, or with the previous absence of chiasmas and crossing over; the former being probably the state of affairs in Datura and Lycopersicum, and the latter perhaps the case in the male Alydus and the male Drosophila. Darlington (1931) has lately shown that *Primula sinensis* keeps some of its nodes till early and middle diaphase.

Conditions of chiasma formation.—On the writer's modified hypothesis, the formation of a chiasma depends on crossing over at a half-twist. But a half-twist will not lead to chiasma formation if the chromomeres are in contact longitudinally; for in this case the flattened ribbon would give way around the point of twisting, and the half-twist would gradually merge into the untwisted part. But if the chromomeres are at a distance apart sufficiently exceeding their breadth, then the half-twist can be all taken up by the connecting fibers at one point, while the adjoining parts of the ribbon take no twist. This is the condition favorable for chiasma formation and crossing over (and also for translocations, etc.). Hence crossing over might perhaps be prevented in an organism by stopping the chromonema from growing sufficiently in length. On the other hand, chiasma formation, crossing over, translocation, etc., might sometimes be increased by any agent that increased the growth in length of the chromonema. With regard to translocation, etc., such increase (by heat, or perhaps by X-rays) might also happen in cells where the chromonema is soon to divide lengthwise for a mitotic division. This perhaps agrees with Muller's results on obtaining translocations by the action of X-rays on the spermatozoa of Drosophila, as well as changes by X-rays in the amount of crossing over in the female (Muller, 1925, 1928).

Chiasmas and crossovers in triploids.—The average number of chiasmas in a specially clear cell of diploid *Tulipa gesneriana* was nearly 2.3. If the chiasma formation in a trivalent is the same as that in a bivalent, there should be apparently 1.5 times this number, or 3.4, chiasmas in a trivalent of Tulipa. On the other hand, if only two homologues synapse at any point in a trivalent, as has been lately assumed by one writer, there might be only 2.3 chiasmas in a trivalent of Tulipa. Plate 3, figure 8, of (Newton and) Darlington's 1929 paper, gives drawings of thirteen trivalents of *Tulipa gesneriana*, at early diaphase, and these apparently have an average of 3.6 chiasmas

to a trivalent. Also figure 9, plate 4, shows ten drawings of trivalents of *T. gesneriana*, at late diaphase, with an average apparently of 3.5 chiasmas to a trivalent. (But these two are not quite random samples.)

If only two chromosomes synapse at once in a trivalent, the crossing over in any chromosome of a triploid might be only two-thirds of that in a corresponding chromosome of the diploid. But, in Drosophila, Redfield (1930) has shown that the total crossing over in the third chromosome of the triploid is about equal to that in the third chromosome of the diploid. Hence we may presume, either that the three chromosomes of a triploid synapse into a triple thread; or, if only two synapse at any one point, that interference is so much decreased that the crossing over is made equal to normal.

Redfield has shown that crossing over in the third chromosome of triploid Drosophila differs from that in the diploid in being increased in the middle and lessened towards the ends of the chromosome; but this change does not seem enough to bring the known mutant genes into regular distribution on the crossover chart. (Bridges and Anderson have also shown a change of crossing over in the first chromosome of the triploid, in which genes which are close in the diploid crossover chart are more separated, and vice versa.) It is a change of the same nature that is shown by Dobzhansky to appear when the ends of translocated parts of chromosomes are marked on the crossover chart, and also on a drawing of the chromosome. This change shows that in the triploid there must be more chiasmas than in the diploid around the central part of the third chromosome, and fewer between the middle part and the ends. Now it has been shown above that the increase of chiasmas near the distal end (or ends) of a chromosome, in a diploid, is probably due to the first internode from the distal end being shorter than the average internode. If the average internode length is lessened, the distribution of the genes in the crossover charts will be somewhat more uniform. But in the triploid there is an excess of chiasmas in one of the three homologues. For the averages of the chiasmas of the 10 trivalents of Tulipa already mentioned were 1.75, 3.5, and 1.75, for the three homologues of a trivalent. The middle homologue has twice as many chiasmas as each of the other two, and therefore twice as much crossing over.

The writer has seen cases of partial triple synapsis in triploid *Hyacinthus orientalis*. Parts of the three homologues were synapsed at zygotene and pachytene, chromomere to chromomere, forming tri-

angles at each locus. In some pachytene cells there was perhaps a large amount of this triple synapsis. (Newton and) Darlington, however, failed to find triple synapsis in a triploid Tulipa.

In triploid Datura (fig. 8), at early diaphase, the chromonemas are

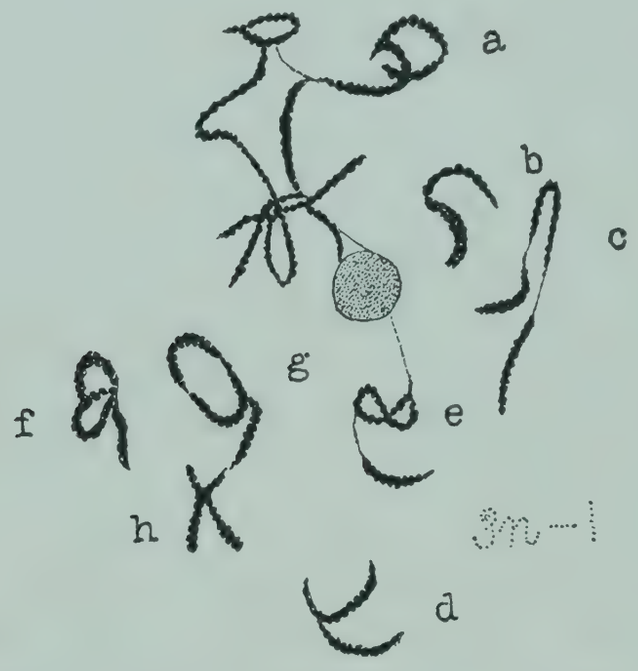


Fig. 8. Camera drawing of a coverglass preparation, in iron-acetocarmine, of a $3n-1$ *Datura stramonium,* at early diaphase. Seven of the trivalents and the bivalent are clear, the four other trivalents overlapping. Some of these may well have come from a triple synapsis. Zigzagging of the chromonemas is distinct. There are one or two nodes, but no unmistakable chiasmas. No secondary split is visible.

already zigzagged, and there are no unmistakable chiasmas. But it appears as if the three homologues of some trivalents, such as *a* and *b* especially, had retained the same curvature, as if they had opened out at diplotene from a triple synapsis. In *d*, figure 8 (the bivalent of this $3n-1$ plant), the two homologues have also the same curve, having doubtless opened out at diplotene from a double synapsis.

CHIASMAS AT DIFFERENT STAGES

(The writer tries to follow E. B. Wilson's latest definitions of these stages. One author of papers on plant chromosomes uses "diplotene" where this paper prefers "early or middle diaphase or diakinesis.")

Nodes at diplotene.—A camera drawing of the upper part of a cell at the beginning of the opening out at early diplotene in *Allium triquetrum* has been given in a previous paper (1931). Such an open-

ing out at very many points has been seen in several liliaceous plants at early diplotene (which is rather a transitory stage, and readily overlooked). Many of these numerous nodes are doubtless not chiasmas, but merely temporary adhesions between the two homologues. Others are probably overlappings. Most of them open out before early diaphase. The nodes found at early diaphase are thus the residue of the numerous nodes seen at early diplotene.

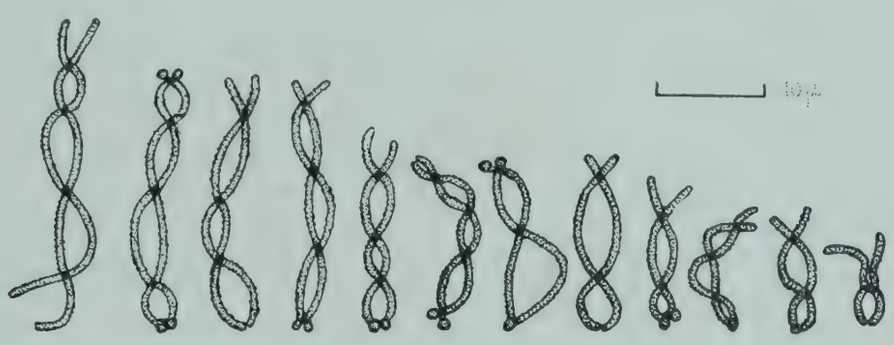


Fig. 9. From a camera drawing of a coverglass preparation of the early diaphase of *Lilium longiflorum*, in iron-acetocarmine. The first two bivalents on the left are probably those with intermediate attachment constrictions, the rest having terminal or subterminal ones. Of the forty-two nodes shown here, thirteen are probably overlapping or adhesions. The bivalents have been oriented so that the short free ends or the terminal junctions are below.

Nodes at early diaphase.—It is difficult to get cells which show well all the nodes of the twelve bivalents in Lilium—in which plant, nodes are well seen. However the writer has obtained two such groups in Lilium, one of which is pictured in figure 9. The numbers of nodes are given below, counting all terminal junctions. (Possible overlappings would also be counted.)

Numbers of nodes	1	2	3	4	5	Totals	Included terminal junctions
L. longiflorum	—	1	4	6	1	43	4
L. regale	—	3	2	5	2	42	2
Averages						42.5	3

Thus the early diaphase of *Lilium longiflorum* showed forty-three nodes, four of which were terminal junctions. The early diaphase of *L. regale* closely resembled this. It has already been noted that the internodes were not excessively short nor usually excessively long, but that their length had the appearance of varying beyond a minimum.

Nodes at middle diaphase.—This stage was observed in *L. longiflorum* to have fewer nodes than early diaphase, and more nodes than

late diaphase. The following counts were made on preparations of *L. regale,* fixed with chromic-acetic-formalin, stained with iron-brazilin, and mounted in immersion oil. (All nodes were counted, but some of them were probably overlappings.)

Numbers of nodes	1	2	3	4	5	Totals	Included terminal junctions
L. regale	—	4	7	1	—	33	2
	—	3	7	2	—	35	2
	1	3	4	3	1	36	3
	—	4	6	2	—	34	2
Averages						34.5	2.3

Thus these averaged eight nodes less per cell than the early diaphase, while the number of terminal junctions was about the same.



Fig. 10. From a camera drawing of a coverglass preparation of the late diaphase of *Lilium longiflorum*, in iron-acetocarmine. The first two bivalents on the left are probably those with intermediate terminal constrictions. Orientation is as in figure 9.

Chiasmas at late diaphase.—These are relatively easy to obtain. In iron-acetocarmine they are readily pressed flat, so that all the nodes can be clearly seen. Figure 10 shows the twelve bivalents in one cell at the late diaphase of *L. longiflorum.*

Numbers of nodes	1	2	3	4	Totals	Included terminal junctions
Lilium longiflorum	1	6	3	2	30	9
	—	6	4	2	32	5
	1	6	5	—	28	4
	2	6	4	—	26	5
	—	7	5	—	29	6
L. speciosum	1	4	5	2	32	3
Averages					29.5	5

These show, on the average, per cell, thirteen nodes less than at early diaphase, and five less than at middle diaphase. There are more terminal junctions.

Chiasmas at metaphase.—Here the bivalents are somewhat contracted, and it is more difficult to be sure that some chiasmas are not omitted than it is at diaphase. The following were counted (fig. 11).

Numbers of nodes..	1	2	3	4	5	Totals	Included terminal junctions
L. longiflorum.....	2	4	4	2	—	30	6
	3	3	4	1	1	30	5
L. regale.....	1	6	3	2	—	30	4
Averages.....						30	5

The average number of chiasmas is about the same as at late diaphase, as is also the number of terminal junctions. Hence we may deduce that a stable number of both nodes and terminal junctions is



Fig. 11. From a camera drawing of the metaphase of *L. longiflorum*, in iron-acetocarmine. Oriented with the attachment fibers above. Alternate internodes darker. The first two bivalents on the left are seen to have intermediate attachments to the spindle fibers. The other ten bivalents show their terminal or subterminal attachment fibers. The number of chiasmas is about the same as in late diaphase.

reached at late diaphase. The gain of terminal junctions at late diaphase and metaphase is probably due to some subterminal chiasmas (while the bivalents were shortening) becoming so shortened as to seem terminal. But this does not account for the true terminal junctions seen at early diaphase, and later.

Hence thirteen nodes out of 42.5 gradually disappear from early diaphase to late diaphase or metaphase. Since metaphase gives the same number of nodes as late diaphase, we may presume that the number has ceased to diminish at late diaphase. This loss of 31 per cent of the number of nodes at early diaphase may be due (1) to some of the nodes at early and middle diaphase having been overlappings, or half-twists caused in part perhaps by the movements of internodes to planes at right angles, each such movement causing a quarter-twist; or (2) to temporary adhesions of the two homologues, like those seen so abundantly at early diplotene. Zigzagging of the chromonemas would prevent sliding of the chiasmas. Hence we may presume that late diaphase and metaphase are free from half-twists, overlappings,

or temporary adhesions of the homologues. As already stated, in many plants and animals, late diaphase and metaphase are free from chiasmas also, and the homologues are then connected by terminal junctions.

Opening out of chiasmas at anaphase.—Here the chiasmas disappear. The paired sister strands which are held together by the attachment constriction (where there is sometimes a special polar corpuscle, as in Agapanthus among flowering plants, and in several animals) pull away together on each side; and the four strands slowly slide over each other and draw out. This drawing out is simple if there is only one chiasma on each side. But most of the bivalents of Lilium and Tulipa have subterminal or terminal primary constrictions, and so the chiasmas have to be drawn out from one end, which is sometimes complicated. In Uvularia this has been seen to lead to chromosome breakage in some cells. Early anaphase, when the strands are well covered with chromatin which smooths out the zigzags of the chromonemas, is a good stage at which to follow the arrangement of the strands at the chiasmas. Unfortunately it lasts only a short time, and so is not common in the preparations. The pulling out at early anaphase is facilitated by the manner in which two chiasmas may run together, as already noted.

Inversion, translocation, etc.—In the "resting" or metabolic stage of the chromosomes of monocotyledons, careful fixation of smear preparations usually discloses coils of very thin threads. In such threads there are sometimes minute chromomeres to be observed soon before division, as seen by Belar (1929) in Tradescantia, and by the writer in the staminal hairs of Rhoeo. Now if one such thread forms a loop on itself, where the two parts of the loop cross there will be an overlapping similar to the half twist at early pachytene. Hence if the chromomeres are far enough apart, the new thread formed by the coming longitudinal split may occasionally connect its chromomeres straight instead of crosswise. In this case one of the threads would be normal, and the other would contain an inverted section.

In a similar way reciprocal translocations could take place between non-homologous overlapping chromonemas whose chromomeres were sufficiently separated. Since in the early stages of most cell divisions the chromosomes are usually arranged with the attachment constrictions next one pole, there is some chance of reciprocal translocations being of about equal lengths. Since at pachytene, and also probably in ordinary metabolic nuclei, the ends of the n or $2n$ chromonemas

are sometimes attached laterally to other threads, as was seen by the writer in Lilium, Aloë, and other liliaceous plants, it is easy to see how terminal translocations might arise. Nor is there any difficulty in explaining large deficiencies by a new transverse junction of chromomeres across a loop in a dividing chromonema.

Thus the writer's modified hypothesis of crossing over can also be applied to the usual phenomena of chromosomal mutation, whether natural or artificial. It has the advantage of not requiring breaks in the chromosomes. *Probably a broken chromosome remains broken.*

SUMMARY

The hypothesis of chiasma formation by alternate openings out was tested by the relevant facts in thirteen cases. In these cases it failed, while the hypothesis of crossing over accompanied by chiasma formation succeeded.

The writer's hypothesis of a half twist followed by the formation of new connecting fibers, fits Anderson's results with the attached first chromosomes of Drosophila, and also fits the facts with regard to the available double chiasmas of Lilium, grasshoppers, etc.

Oblique chiasma formation was absent in the thirteen clear cases of consecutive chiasmas that were available. Hence, from the average number of chiasmas the average amount of crossing over can be calculated, and the reverse. The first was done with nine cells of Lilium at late diaphase or metaphase; and the second with the first chromosome of Drosophila.

Instead of three times as many long as short free terminal internodes of bivalents of Lilium, there were found forty-three long to fifty-three short for the ten bivalents with terminal or subterminal attachment constrictions, in ten diaphase cells. The distal ends of three cells at metaphase gave fourteen long to twenty-eight short. Hence chiasma formation and crossing over occurred more frequently not far from the distal ends of these bivalents than elsewhere in the bivalents.

The lengths of the internodes at early diaphase having been measured, there were found a minimum of nine units, an average of fifteen units, and a maximum of twenty-eight units, in thirty-one internodes. This seems in accordance with a modal length of internode, with longer range above than below. (These lengths must be somewhat increased, because of the occurrence of temporary nodes.)

Terminal junctions, where only a fine thread connects the ends of the chromosomes, are not chiasmas, but may (or may not) have once been chiasmas.

Bivalents of plants like Datura, which usually show no chiasmas at diaphase or metaphase, but only terminal junctions, may have opened out at diplotene instead of, as is most usual in *liliaceous* plants, at anaphase.

Half-twists would not lead to chiasma formation and crossing over if the chromomeres were too close together. Hence possibly agencies which increase crossing over may do so by causing the chromonema to grow longer.

In a triploid Hyacinthus, at zygotene and pachytene, there were sometimes three threads synapsed, chromomere to chromomere, forming a series of triangles.

The nodes (31 per cent) at early diaphase in Lilium, which are lost during diaphase, may be either overlappings or temporary adhesions.

The increase of apparent terminal junctions during diaphase (by about two per cell) is probably due to the shortening of subterminal chiasmas. True terminal junctions (about three per cell) apparently do not alter during diaphase.

Translocations, reciprocal translocations, inversions, and large deficiencies are explained by the writer's modified hypothesis of crossing over.

The observed synapsis of short parts of the chromosomes of Rhoeo tends to confirm the writer's hypothesis of segmental interchange (reciprocal translocation) as accounting for rings of chromosomes in Rhoeo, Oenothera, Zea, Pisum, Datura, etc. (Cf. also Sturtevant and Dobzhansky, 1930.)

LITERATURE CITED

ALTENBURG, E.

1921. Interference in *Primula sinensis*. Am. Nat., vol. 55, pp. 78–80.

ANDERSON, E. G.

1925. Crossing over in a case of attached X chromosomes in *Drosophila melanogaster*. Genetics, vol. 10, pp. 403–417.

BELAR, K.

1929*a*. Untersuchungen an den Spermatocyten von Chorthippus. . . . . W. R. Archiv. f. Entwickelungsmech. . . . ., vol. 118, pp. 359–484.

1929*b*. Untersuchungen an den Staubfadenhaarzellen. . . . . Zeitsch. f. Zellforsch. . . . ., vol. 10, pp. 73–134.

BELLING, J.

1925. Homologous and similar chromosomes in diploid and triploid hyacinths. Genetics, vol. 10, pp. 59–71.

1926. Single and double rings at the reduction division in Uvularia. Biol. Bull., vol. 50, pp. 355–363.

1927. Configurations of bivalents of Hyacinthus. . . . . Biol. Bull., vol. 52, pp. 480–487.

1928. Nodes and chiasmas in the bivalents of Lilium. . . . . Biol. Bull., vol. 54, pp. 465–470.

1929. Nodes and internodes of trivalents of Hyacinthus. Univ. Calif. Pub. Bot., vol. 14, pp. 379–388.

1930. The secondary split in the maturation divisions of liliaceous plants. Nature, vol. 125, p. 52.

1931. Chromomeres of liliaceous plants. Univ. Calif. Pub. Bot., vol. 16, pp. 153–170.

BLAKESLEE, A. F., *et al.*

1927. Mutations in a haploid Datura. Jour. Hered., vol. 18, pp. 193–199.

BRIDGES, C. B., and ANDERSON, E. G.

1925. Crossing over in the X-chromosomes of triploid females of *Drosophila melanogaster*. Genetics, vol. 10, pp. 418–441.

DARLINGTON, C. D.

1930. A cytological demonstration of genetic crossing over. Proc. Roy. Soc., B, vol. 107, pp. 50–59.

1931. Meiosis in diploid and tetraploid *Primula sinensis*. Jour. Genet., vol. 24, pp. 65–96.

DOBZHANSKY, T.

1929. Genetical and cytological proof of translocations involving the third and fourth chromosomes of *Drosophila melanogaster*. Biol. Zentralbl., vol. 49, pp. 408–419.

1930. Cytological map of the second chromosome of *Drosophila melanogaster*. Biol. Zentralbl., vol. 50, pp. 671–685.

GELEI, J.

1921. Weitere Studien über die Oogenese des *Dendrocoelum lacteum*. Arch. Zellf., vol. 16, pp. 88–169.

Janssens, F. A.
1905. Évolution des auxocytes mâles du *Batrachoseps attenuatus.* Cellule, vol. 22, pp. 377–427.
1909. La théorie de la chiasmatypie. Cellule, vol. 25, pp. 387–411.
1924. La chiasmatypie chez les insectes. Cellule, vol. 34, pp. 133–359.

Maeda, T.
1930*a*. The meiotic divisions in pollen mother cells of the sweet-pea. . . . . Mem. Coll. Sci. Kyoto Imp. Univ., B, vol. 5, pp. 89–123.
1930*b*. On the configurations of gemini in the pollen mother cells of *Vicia faba* L. *Ibid.*, pp. 125–137.

Matsuura, H.
1929. A bibliographical monograph on plant genetics (Tokyo Imp. Univ.), pp. 1–499.

Morgan, T. H.
1924. The bearing of genetics on the cytological evidence for crossing over. Cellule, vol. 36, pp. 113–123.
1926. The theory of the gene (Yale Univ. Press), pp. 1–343.

Muller, H. J.
1925. The regionally differential effect of X-rays on crossing-over in autosomes of Drosophila. Genetics, vol. 10, pp. 470–507.
1928. The production of mutations by X-rays. Proc. Nat. Acad. Sci., vol. 14, pp. 714–726.

Newton, W. C. F.
1927. Chromosome studies in Tulipa. . . . . Linn. Soc. Jour. Bot., vol. 47, pp. 339–354.

Newton, W. C. F., and Darlington, C. D.
1929. Meiosis in polyploids. Jour. Genet., vol. 21, pp. 1–56.
1930. *Fritillaria meleagris:* chiasma formation and distribution. *Ibid.*, vol. 22, pp. 1–14.

Redfield, H.
1930. Crossing over in the third chromosomes of triploids of *Drosophila melanogaster.* Genetics, vol. 15, pp. 205–252.

Reuter, E.
1930. Beiträge zu einer einheitlichen Auffassung gewisser Chromosomenfragen. . . . . Act. Zool. Fennica, vol. 9, pp. 1–487.

Robertson, W. R. B.
1916. Chromosome studies I. Jour. Morph., vol. 27, pp. 179–332.

Sax, K.
1930. Chromosome structure and the mechanism of crossing over. Jour. Arnold Arboretum, vol. 11, pp. 193–220.

Sturtevant, A. H.
1928. A further study of the so-called mutation at the bar locus of Drosophila. Genetics, vol. 13, pp. 401–409.

Sturtevant, A. H., and Dobzhansky, T.
1930. Reciprocal translocations in Drosophila, and their bearing on Oenothera cytology and genetics. Proc. Nat. Acad. Sci., vol. 16, pp. 533–536.

Wenrich, D. H.
1916. The spermatogenesis of *Phrynotettix magnus.* . . . . Bull. Mus. Comp. Zool. (Harvard), vol. 60, pp. 57–135.

CHROMOSOME STUDIES IN THE CUCURBITACEAE

BY

J. W. McKAY

University of California Publications in Botany
Volume 16, No. 9, pp. 339–350, 30 figures in text
Issued June 19, 1931

University of California Press
Berkeley, California

Cambridge University Press
London, England

CHROMOSOME STUDIES IN THE CUCURBITACEAE

BY
J. W. McKAY

INTRODUCTION

This paper is concerned chiefly with a detailed consideration of chromosome numbers in the Cucurbitaceae, which was outlined briefly in an earlier report (McKay, 1930). In that report it was stated that chromosome counts of species of Cucurbitaceae found in the literature at that time were confined largely to the cultivated forms of economic importance. This paper deals mainly with wild species of cucurbits, although several forms studied are found in the trade to some extent.

For some years the writer has been carrying on genetic work on the inheritance of seed characteristics in *Citrullus,* but, owing to the length of time necessary to establish pure lines, no definite results have been realized. This, together with other breeding experiments being carried on with *Cucurbita,* having definitely centered the author's interest in the group, seemed to justify a broader attack on the family, hence the present work. It was thought that a cytological examination of as many species as possible might be the means of discovering relationships that hitherto had not been realized. On the basis of modern cyto-taxonomic investigation of plant groups such, for example, as is presented for the genus *Crepis* by Babcock and Navashin (1930), it would seem probable that such relationships might be brought to light. While cytological findings have not been of great value in the present work in showing further affinity between species and genera, certain instances have arisen where a study of the chromosomes of a plant have been useful in determining its relationship to other species. The taxonomic side has not been considered, largely because so little has been contributed by cytological study that is of value in placing species and genera into more natural groups.

RECENT CYTOLOGICAL STUDIES IN THE CUCURBITACEAE

Whitaker (1930) has recently published an account of his results in determining the chromosome numbers of the cultivated cucurbits. Since his results are in accord with those of Passmore (1930), it seems probable that the lack of agreement among earlier workers as to the chromosome number in certain forms, particularly *Cucurbita,* is cleared up by these later determinations. Whitaker gives a table which summarizes the work that has been done on chromosome number in the cultivated cucurbits, and also in his summary lists the species with which he worked and the number of chromosomes determined for each.

The work of Passmore (1930) describes microsporogenesis in *Cucurbita pepo* L. (Jersey White Bush squash) in detail, and points out the chief differences noted in other species, namely: *C. maxima, Citrullus vulgaris, Luffa cylindrica, Cucumis melo* and *C. sativus.* A table is given which summarizes the reported chromosome numbers in the family.

Kozhukhow (1930) reports an exhaustive survey of the somatic chromosomes of the genus *Cucumis,* and finds that, with the exception of the cucumber, *Cucumis sativus,* which has the $2n$ number of 14, all species have 24 somatic chromosomes. He believes with Levitsky that the melon forms of *Cucumis* have arisen from the cucumber by a process of chromosome fragmentation. This process is spoken of as "Karyophylogeny."

Kozhukhow (1925) in an earlier paper figures the somatic chromosomes of the more important cultivated cucurbits, and his counts of the species of *Cucurbita* differ from those recorded by later workers, as shown in table 1. As stated above, it is to be regarded as probable that agreement by recent investigators on the chromosome number of these forms lends strength to the authenticity of these later counts.

MATERIALS AND METHODS

Seeds of most of the plants were obtained through exchange lists of various botanical gardens throughout the world, although several species were obtained through the larger commercial seed firms.

Root tips were fixed 12–24 hours in Karpechenko's solutions made up as follows: solution A: 65 cc water, 10 cc glacial acetic acid, 1 gram chromic acid; solution B: 35 cc water, 40 cc commercial formalin (40 per cent stock solution). Equal quantities of solutions A and B are mixed immediately before placing the material in the killing fluid. Anthers and young flower buds were fixed in this mixture after first having been placed for 1–2 minutes in Carnoy's fluid.

All material was imbedded in paraffin, sections cut from 7–12 microns in thickness, and stained in Haidenhain's iron-haematoxylin.

CHROMOSOME NUMBER IN THE CUCURBITACEAE

In studying the somatic chromosomes of the various species it has been found convenient to group together all those which have the same number, but it is to be borne in mind that this grouping has no significance other than as a matter of convenience.

The first six figures show the somatic chromosomes of the species which have the diploid number 22. *Lagenaria vulgaris,* the bottle gourd (fig. 1), in the author's previous paper was reported to have 24 somatic chromosomes, but further study revealed only 22. Very few differences are noted in the chromosomes of this group, differences in size forming the chief distinction. Indeed, it is true throughout the family that a remarkable uniformity of chromosome shape is met with, small differences in size and differences in number being the chief way in which chromosomes of one species differ from those of another. This stable condition is somewhat suggestive of that found in the genus *Rhododendron* by Sax (1930), although his conclusions were based on chromosome number alone determined from smears of pollen mother cells.

Figure 7 shows the chromosomes of *Cucurbita ficifolia* Bouché (Malabar gourd) which is somewhat related to the cultivated species of *Cucurbita.* Figures 8, 9, and 11 show the somatic chromosomes of

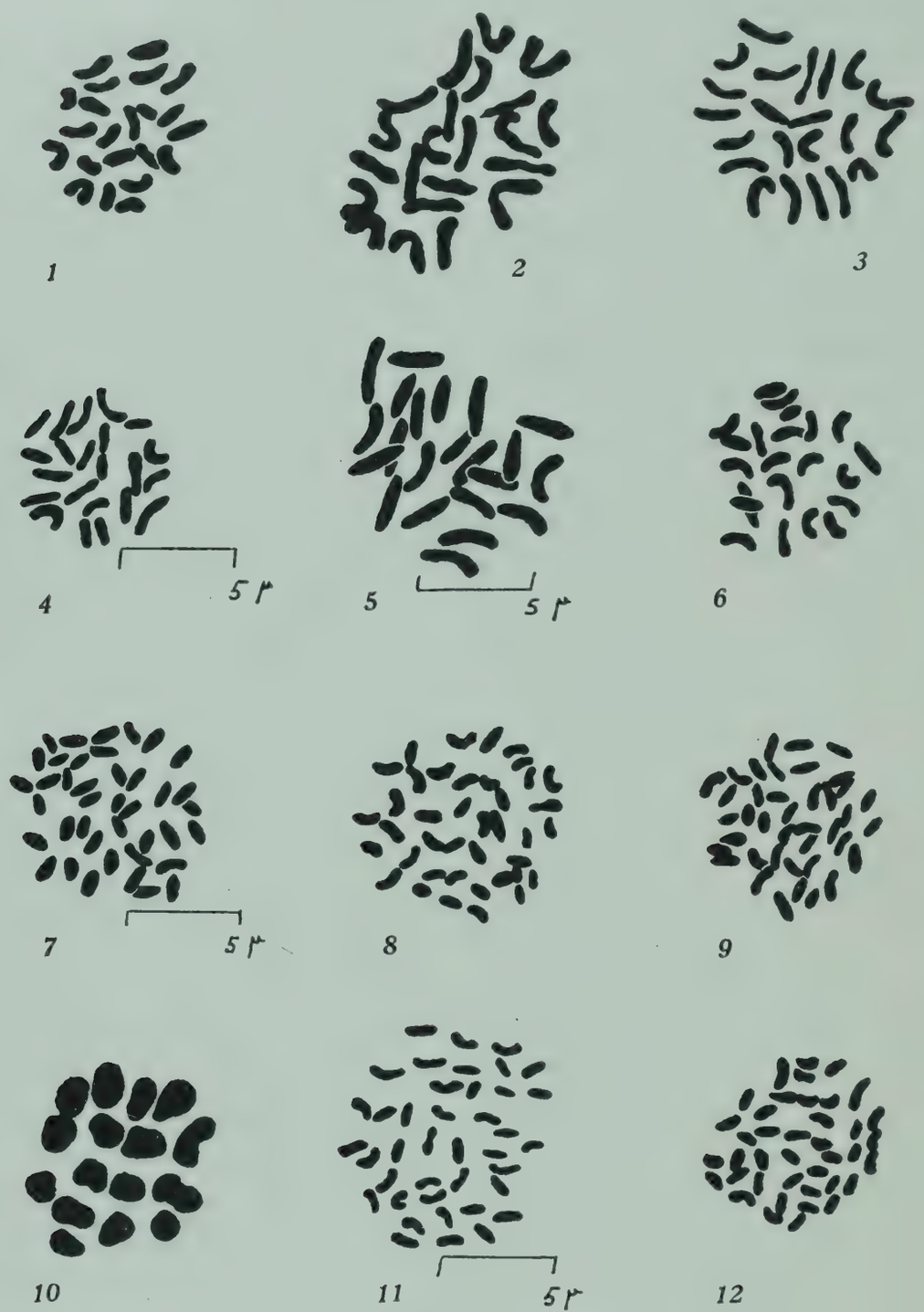


Fig. 1–12

All drawings were made with the aid of a camera lucida and a Leitz microscope equipped with a 1.95 mm oil immersion objective, apert. 1.32, 1/12*a*, and 15*x* Hyperplane oculars. Figures 25, 26, 28, 29, 30, × 1760; figure 27, × 1100; all other figures × 2500.

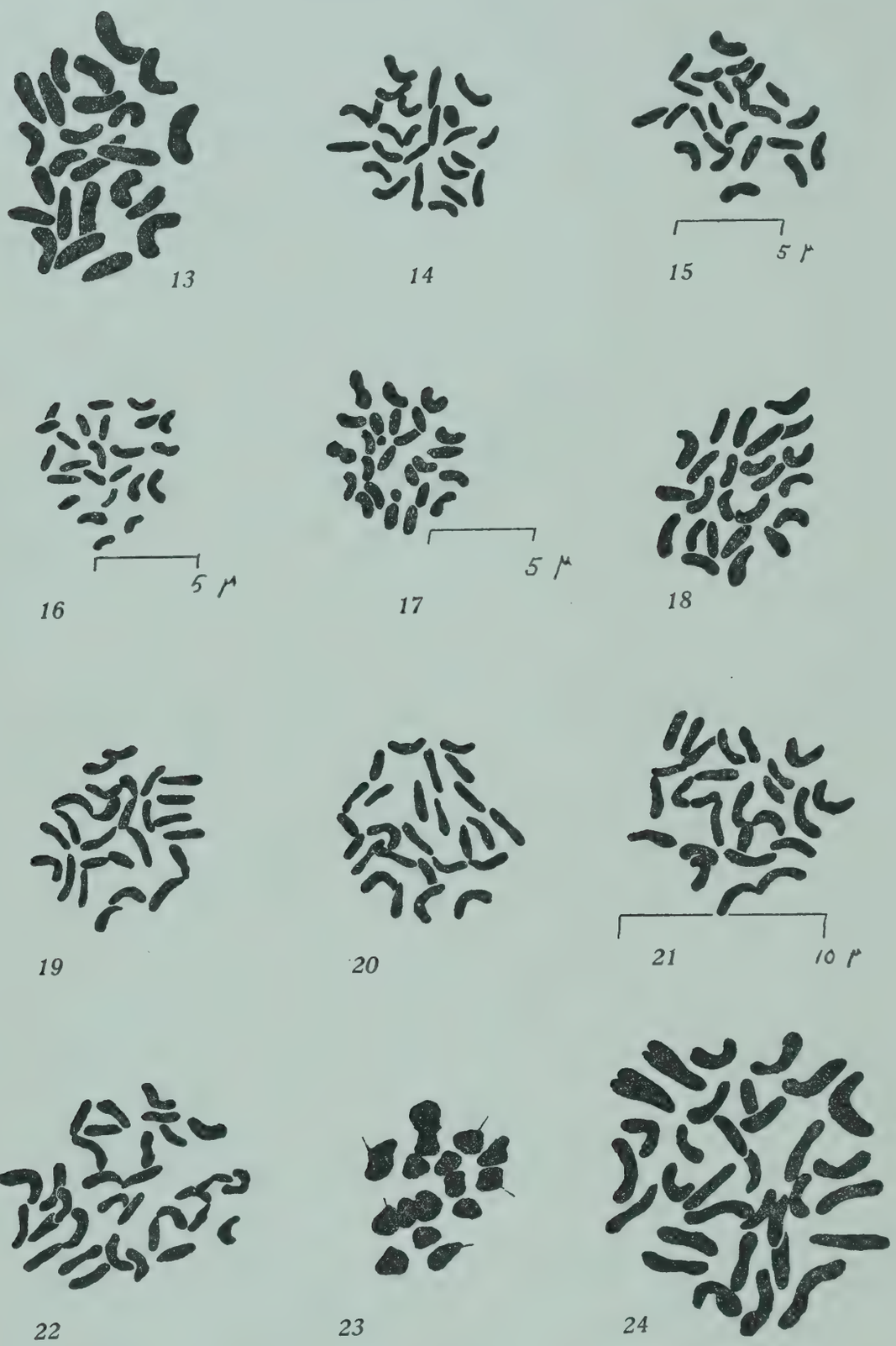
Somatic and meiotic chromosomes of cucurbit species:

1. *Lagenaria vulgaris* $2n = 22$
2. *Tricosanthes Anguina* $2n = 22$
3. *Gymnopetalum leucosticum* $2n = 22$
4. *Momordica Charantia* $2n = 22$
5. *Ibervillea lindheimeri* $2n = 22$
6. *Momordica balsamina* $2n = 22$
7. *Cucurbita ficifolia* $2n = 40$
8. *Cucurbita palmata* $2n = 40$
9. *Cucurbita foetidissima* $2n = 40$
10. *Cyclanthera explodens* $n = 16$
11. *Cucurbita digitata* $2n = 40$.
12. *Benincasa cerifera* (*Cucurbita* sp.) $2n = 40$

the three wild species of *Cucurbita* found in southwestern United States to be the same as the cultivated members of *C. pepo* and *C. maxima,* namely $2n = 40$. Attention is here called to the fact that in the author's previous paper the diploid number for three species, *C. ficifolia* Bouché, *C. foetidissima* H.B.K., and *C. Palmata* Wats., was reported as 42, but on further study of root-tip cells, with a check of the meiotic count in *C. palmata* (fig. 27), the somatic number is found to be 40 for all three species. It is worthy of note that *C. foetidissima, C. palmata,* and *C. digitata* Gray are very similar taxonomically, differences in the lobing of the leaves forming the chief distinction as indicated by the specific names, and this close relationship is borne out by the similarity of the chromosomes.

There are two species of the genus *Benincasa* mentioned in exchange seed lists of botanical gardens, *B. hispida* Cogn. and *B. cerifera* Savi. These names are regarded by many authors as synonyms, but seeds coming to this laboratory under the two names were in a few instances obviously very different and could not represent a single species. Plants grown from seeds of *B. hispida* were identified as the "Chinese watermelon" or "Zit-kwa" grown so extensively by the Chinese and Japanese. The $2n$ number of this plant is 24, and the chromosomes are fairly large and uniform in shape, as shown in figure 13. The plants produced from seeds received under the name *B. cerifera* Savi, however, resembled very closely some species of *Cucurbita,* especially forms of *C. moschata.* The only morphological feature which this species has in common with *B. hispida* is the foliate nature of the sepals, a character which distinguishes the genus from others in the family. The chromosomes are unmistakably like those of the Cucurbita group in both number and shape, and it is suggested that this plant, perhaps through mistake, has been carried under the name *B. cerifera* Savi on the basis of its foliate sepals without regard to its affinities in other respects to the *Curcurbita* group where it doubtless belongs.

The 24-chromosome group is considered next, and figures 13–18 are drawings taken from root-tip cells in the metaphase of division. With the exception of *Benincasa hispida,* which has fairly large chromosomes, these species again show very few morphological and size differences in their chromosome complements. *Melothria punctata* L. (fig. 17), is the single species of all examined which exhibits satellited chromosomes, and in this form one pair is observed to have large satellites. Considerable size differences are noted between the chromo-



Figs. 13–24

Somatic and meiotic chromosomes of cucurbit species:

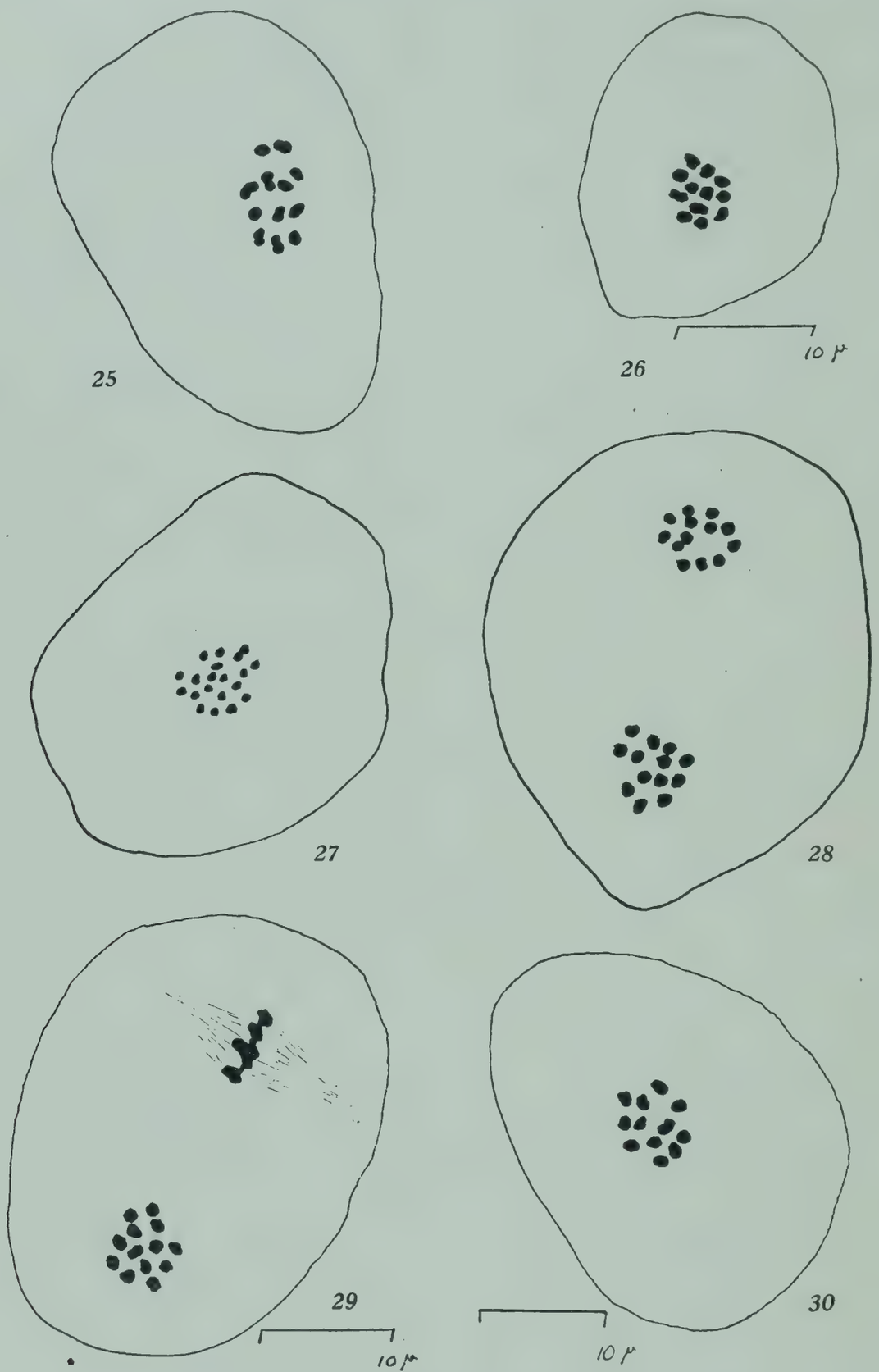
13. *Benincasa hispida* $2n = 24$
14. *Sicyos angulatus* $2n = 24$
15. *Bryonopsis laciniosa* $2n = 24$
16. *Ibervillea sp.* $2n = 24$
17. *Melothria punctata* $2n = 24$
18. *Coccinia hirtella* $2n = 24$
19. *Luffa marylandica* $2n = 26$
20. *Luffa acutangula* $2n = 26$
21. *Luffa gigantea* $2n = 26$
22. *Echinocystis fabacea* $2n = 32$
23. *Echinocystis fabacea* $n = 16$
24. *Cyclanthera pedata* $2n = 32$

somes of the undetermined species of *Ibervillea* shown in figure 16 which has 24 chromosomes, and those of *I. lindheimeri* Gray previously referred to in a discussion of the 22-chromosome group, and illustrated in figure 5.

The genus *Luffa,* which includes the vegetable sponges or dish-cloth gourds, presents a condition which may require further study before a thorough knowledge of the group is obtained. Passmore (1930) gives the haploid number of 11 for *L. cylindrica.* The present writer, working with three forms under the names *L. marylandica, L. gigantea* and *L. acutangula,* finds the haploid number for these forms to be 13, as shown by both somatic and meiotic counts, except in the case of *L. marylandica,* for which only the somatic count is available (figs. 19, 20, 21, 28, and 29). Along with seeds of these three species obtained from the firm of Haage and Schmidt, Erfurt, Germany, seeds of two other species of *Luffa* were included, *L. cylindrica* and *L. aegyptiaca.*

The author was not successful in growing plants of the latter two species to maturity, and root-tip material from them is scanty, but a summary examination of root-tip cells of these two forms indicates a haploid number of 13, similar to the three species reported above. These preliminary results do not agree with those of Passmore, who gives a haploid number of 11 for *L. cylindrica.* The present writer is of the opinion that there is considerable confusion in the nomenclature of this genus, and that further work should be done in eliminating certain names or recognizing them as varieties. For example, the writer is inclined to believe that the five names mentioned above represent no more than three good species, possibly two. *L. acutangula* is certainly a species apart from the others, and *L. aegyptiaca* is probably a good species, although only one plant has come under observation so far, but the other three are certainly very similar in external morphology. However, mature fruits were not obtained in the case of *L. cylindrica.*

Two genera are represented in the 32-chromosome group, *Cyclanthera* and *Echinocystis* (*Micrampelis*), both of which occur in the Cyclanthera tribe. This is the only example in the family where a definite taxonomic group is also set apart from other members of the family on the basis of chromosome number. Only one species of *Echinocystis* is figured, *E. fabacea* Naud. (figs. 22 and 23), although two other species were examined and found to have 32 somatic chromosomes (*E. oregana* Cogn. and *E. macrocarpa* Greene). The chromo-



Figs. 25–30

Meiotic chromosomes of cucurbit species:

25. *Sicyos angulatus* $n = 12$
26. *Melothria punctata* $n = 12$
27. *Cucurbita palmata* $n = 20$
28. *Luffa acutangula* $n = 13$
29. *Luffa gigantea* $n = 13$
30. *Coccinia hirtella* $n = 12$

somes of *Cyclanthera pedata* Schrad. are the largest of any species studied, and offer the nearest approach to recognizable morphological differences that is met with in any form examined (fig. 24). The 16 bivalent chromosomes of *C. explodens* Naud. are seen in figure 10.

Table 1 gives a complete summary of the chromosome numbers reported for species of Cucurbitaceae to date, with the exception of a few species of *Cucumis* given by Kozhukhow (1930).

DISCUSSION

Perhaps the most striking feature resulting from a survey of the chromosomes of a number of cucurbit species is the uniformity of size and shape of chromosomes. This may be regarded as unusual in view of the great amount of diversity exhibited by the species examined.

Three groups of species are set apart cytologically from the majority of forms, the Cyclanthera tribe, the genus *Cucurbita,* and the single polymorphic species *Cucumis sativus.* All species of the Cyclanthera tribe examined show 16 pairs, which are larger and show more definite morphology than any species studied. The genus *Cucurbita,* although occupying a position in the Cucurbita tribe along with many other genera, may be regarded as having diverged some distance from them on the basis of the numerous and very small chromosomes carried by its species.

The cucumber, of course, occupies a unique position in the family on account of its low chromosome number. It is stated above that Kozhukhow considers the chromosomes of other species of *Cucumis* to have arisen by fragmentation from those of the cucumber. If this process is to be considered as taking place with particular regard to the cultivated species of curcubits, the suggestion might well be further extended to include the species of *Cucurbita* as having arisen through fragmentation of chromosomes of *Cucumis melo* and accompanying phylogenetic differentiation. Species of *Cucurbita* resemble the melon forms of *Cucumis melo* much more closely than they do other cucurbit species, and the chromosomes of species of *Cucurbita* are small and numerous enough to have arisen through fragmentation of melon chromosomes.

The present author, however, would prefer to account for the origin of American forms of *Cucurbita* by some other process which would allow an independent origin apart from *Cucumis.* This may have

TABLE 1

spp.	*n*	2*n*	reported by
Benincasa cerifera (*Cucurbita* sp.)	....	40	Author
Benincasa hispida	....	24	Author
Bryonia alba	10	....	Böenicke, Meurman
Bryonia dioica	10	....	Strasburger, Meurman
Bryonopsis laciniosa	....	24	Author
Citrullus vulgaris	11	22	Kozhukhow, Whitaker, Passmore
Coccinia hirtella	12	24	Author
Cucumis Anguria	11	....	Whitaker
Cucumis dipsaceus	....	24	Kozhukhow, Author
Cucumis melo	12	24	Kozhukhow, Author, Whitaker, Passmore
Cucumis metuliferus	....	24	Kozhukhow, Author
Cucumis myriocarpus	....	24	Kozhukhow, Author
Cucumis sativus	7	14	Kozhukhow, Whitaker, Passmore
Cucurbita digitata	....	40	Author
Cucurbita ficifolia	....	40	Author
Cucurbita foetidissima	....	40	Author
Cucurbita maxima	24	....	Kozhukhow
Cucurbita maxima	20	....	Castetter, Whitaker, Passmore
Cucurbita moschata	24	....	Kozhukhow, Whitaker
Cucurbita pepo	12	....	Lundegardh
Cucurbita pepo v. *pomiformis*	20	....	Kozhukhow
Cucurbita pepo v. *citrullina*	21	....	Kozhukhow
Cucurbita palmata	20	40	Author
Cyclanthera explodens	16	....	Author
Cyclanthera pedata	....	32	Author
Ecballium elaterium	....	24	Author
Echinocystis (*Micrampelis*) *fabacea*	16	32	Author
Echinocystis lobata	16	....	Kirkwood
Gymnopetalum leucosticum	....	22	Author
Ibervillea lindheimeri	....	22	Author
Ibervillea sp.	....	24	Author
Lagenaria vulgaris	11	22	Whitaker, Author
Luffa acutangula	13	26	Author
Luffa gigantea	13	26	Author
Luffa cylindrica	11	22	Passmore
Luffa marylandica	....	26	Author
Melothria punctata	12	24	Author
Momordica Charantia	....	22	Author
Momordica balsamina	....	22	Author
Sicyos angulatus	12	24	Author

come about through hybridization between species with $2n = 20$ followed by amphidiploidy (doubling of the haploid sets contributed by the parents). Such species may still exist in the American tropics, although they may have become altered through change of chromosome number accompanied by morphological divergence.

Perhaps further discussion is uncalled for in this brief paper; yet, if chromosome number is to be considered in connection with the mode of origin of American forms of *Cucurbita,* the latter explanation in the author's opinion seems best to fit in with the fact that these forms are known to be native to the American continents (Erwin, 1931).

SUMMARY

1. A discussion is given of the chromosome size, number and morphology of 22 species of cucurbits, and for convenience in discussion the species are grouped according to chromosome number.

2. The range of chromosome numbers now reported for the family, the haploid numbers being given, is as follows: 7, 10, 11, 12, 13, 16, 20, 24.

3. An instance is cited in the case of *Benincasa cerifera* Savi in which a study of chromosome number and morphology is of value in determining the approximate taxonomic affinity of a species.

4. Attention is called to the situation existing in the genus *Luffa* in which the chief difficulty seems to be the uncertainty of being able to identify the forms with which one may be working.

5. Hybridization of existing or preexisting forms of *Cucurbita* followed by amphidiploidy is suggested as the possible method by which the present-day species of this genus may have arisen. This method is in harmony with the fact that the majority of these forms are known to be native to the American continents.

6. A table is given which summarizes the chromosome numbers reported for cucurbit species at the present time.

ACKNOWLEDGMENTS

The writer wishes to express his appreciation to Professor E. B. Babcock for advice and kindly criticism in the preparation of this paper, and to Dr. T. H. Goodspeed for aid in securing seeds of many of the species studied.

LITERATURE CITED

Babcock, E. B., and Navashin, M.
1930. The genus *Crepis*. Bibl. Genetica, vol. 6, pp. 1–90.

Böenicke, L. von
1911. Zur Kenntnis der Prophasen der heterotypischen Teilung einiger Pollenmutterzellen. Ber. Deutsch. Bot. Ges., vol. 29, pp. 59–65.

Castetter, E. F.
1926. Microsporogenesis in *Cucurbita maxima*. Amer. Jour. Bot., vol. 13, pp. 1–10.

Erwin, A. T.
1931. Nativity of the Cucurbits. Bot. Gaz., vol. 91, pp. 105–108.

Heimlich, L. F.
1927. Microsporogenesis in the cucumber. Proc. Nat. Acad. Sci., vol. 13, pp. 113–115.

Kirkwood, J. E.
1907. Some features of pollen formation in the Cucurbitaceae. Bull. Torr. Bot. Club, vol. 34, pp. 221–242.

Kozhukhow, S. A.
1925. Karyotypische Eigentümlichkeiten der kultivierten Cucurbitaceae. Bull. Appl. Bot. Pl. Breed., vol. 14, pp. 89–96.
1930. Karyological investigations of the genus *Cucumis*. Bull. Appl. Bot. Pl. Breed., vol. 23, pp. 357–366.

Lundegårdh, H.
1914. Zur Kenntnis der heterotypischen Kernteilung. Arch. Zell., vol. 13, pp. 145–157.

McKay, J. W.
1930. Chromosome numbers in the Cucurbitaceae. Bot. Gaz., vol. 89, pp. 416–417.

Meurman, O.
1925. The chromosome behavior of some dioecious plants and their relatives with special reference to sex chromosomes. Soc. Sci. Fennic. Commentat. Biol., vol. 2, pp. 1–104.

Passmore, Sara F.
1930. Microsporogenesis in the Cucurbitaceae. Bot. Gaz., vol. 90, pp. 213–223.

Sax, Karl.
1930. Chromosome stability in the genus *Rhododendron*. Amer. Jour. Bot., vol. 17, pp. 247–251.

Strasburger, E.
1910. Ueber geschlechtbestimmende Ursachen. Jahrb. Wiss. Bot., vol. 48, pp. 427–520.

Whitaker, Thomas W.
1930. Chromosome numbers in the cultivated Cucurbits. Amer. Jour. Bot., vol. 17, pp. 1033–1040.

SOME EARLY ALGAL CONFUSIONS

BY

WILLIAM ALBERT SETCHELL

University of California Publications in Botany
Volume 16, No. 10, pp. 351–366, pl. 31
Issued September 16, 1931

University of California Press
Berkeley, California

Cambridge University Press
London, England

SOME EARLY ALGAL CONFUSIONS

BY

WILLIAM ALBERT SETCHELL

While attempting to make certain of various points connected with the early taxonomic history of sundry marine algae under investigation, there came to light some several matters in connection with the application of the various views on nomenclature which had, of necessity, to be explored farther and the way made straight for further procedure. Since these concern the earlier writers in our botanical literature and since later writers seem largely to have failed properly to evaluate their methods of procedure and their points of view, it may not be superfluous to remind the younger generation, at least, of the activities of this earlier group of botanists who, either incidentally or primarily, proposed specific or generic names for algae, but also concerned themselves with attempting some kind of a classification.

The first edition of the Species Plantarum of Linnaeus (vols. 1, 2, 1753) is the starting point for algae in general. Certain groups have a later incipience, but they will not be of concern to the subject matter of this article. Our earlier botanists, however, not being so extraordinarily concerned with priority as is the present generation, quoted either what they considered as the standard edition, or, most often, perhaps the one each happened to have at hand. In most cases, this happened to be the second edition of the Species Plantarum (vol. 1, 1762; vol. 2, 1763). Later writers, assuming that the quotations of these earlier writers were from the first edition, have often assisted in "creating confusion," or extending an erroneous opinion expressed or implied by others. The twelfth edition of the Systema Naturae, in 1767, partly supplanted, partly extended, as to additional species in particular, both editions of the Species Plantarum. While the species of Linnaeus are described very briefly and seldom discussed, there are, so far as the algae are concerned, certain helps provided for their identification.

The Linnaean herbarium, purchased from the heirs of Linnaeus by Sir James Edward Smith, is now in the possession of the Linnaean Society of London. An index, with qualifying marks, compiled and arranged by Benjamin Daydon Jackson, was issued by the Linnaean Society in 1912. By the numbers appended to the species names in this list, it is possible to determine whether the specimen of the plant enumerated was in the herbarium in 1753 (date of the first edition of the Species Plantarum), added to it, or at least noted, in 1755, or was in place in 1767 (date of Systema Naturae, ed. 12, vol. 2, Vegetabilia).

References to earlier literature are appended, as illustrating what the specific name is supposed to cover. When illustrations, of reasonable accuracy, are quoted, this is certainly of great service. In algae, references to Ray and to Morison are of assistance, since the herbaria of both are preserved and Ray refers to certain older collections now in the British Museum (to be noted later on) and Morison's figures are fair to excellent.

It may be noted, in passing, that Linnaeus seems to have been less successful in his treatment of the algae (as now limited) than of any of the groups of plants (see Goodenough and Woodward, 1795, pp. 87, 88) and the same may be said of Gmelin (1768), who issued the first work devoted to the algae. Gmelin's figures, in general, are inexact and as Goodenough and Woodward (1797, p. 86) indicate, he was not certain of the Linnaean species. William Hudson (Gulielmus Hudsonus, 1730–1793) was the first to establish binomials for a considerable number of the algae, as well as to outline a more intelligent arrangement than had existed before his time (see Goodenough and Woodward, p. 88).

Hudson's Flora Anglica was first published in 1762, but a second edition, augmented, corrected, and otherwise improved, was put forward by him in 1778. It is this superior edition which is commonly quoted by his contemporaries and immediate successors and so much so that the earlier edition has largely passed from the notice of later writers. A posthumous edition, scarcely differing from the second, was issued in 1798. This is often quoted for authority. Hudson, who was an apothecary, of the Society of the Apothecaries, and for a time connected with the Physic Garden at Chelsea, seems to have been most careful as to his citations and their verification. Hudson may be considered from the point of view of elucidator of the algae of the works of Robert Morison and of John Ray.

Robert Morison (1620–1683), the predecessor of Ray and the critic of Caspar Bauhin, illustrated a fair number of marine algae in the plates (8–10) of the third volume of his Plantarum Historiae Universalis Oxoniensis (1715), most of which, admirably delineated for that time, are clearly recognizable. Ray, apparently, relied much on these plates and their attendant diagnoses by Morison.

John Ray succeeded Morison and preceded Linnaeus and Hudson. He was a most methodical man and gave full credit to all his predecessors. The algae enumerated or described in his various works, were especially based on Morison's figures and on certain dried specimens contained in various collections, fortunately preserved to us (at the British Museum of Natural History) through the foresight and munificence of Sir Hans Sloane, of Sir Joseph Banks, and of others.

Samuel Goodenough (1743–1827) was a clergyman, finally Bishop of Carlisle, an ardent botanist with a fine analytic mind. In 1795 he, in collaboration with Thomas Jenkinson Woodward (1745–1820), presented to the Linnean Society of London, of which he was one of the trustees, a series of Observations on the British Fuci, with Particular Descriptions of Each Species. This paper is of extreme importance in connection with early usage and ideas among the algae, since it is based upon a critical examination of each one of the seventy-two species considered, especially as to identity with species previously described. The authors appear to have carefully compared the plants assigned under each species with the type specimens of the Linnean herbarium or with the plants cited by Ray and by Hudson. Besides the opportunities afforded by the Linnean herbarium in the possession of the Linnean Society of London, they explicitly refer to the "old Herbaria preserved in the British Museum," as sources of their findings. These are, in particular, those of Buddle, Petiver, Uvedale, Vernon, Floyd, Cowrton, and others (Linn. Soc. Trans., 3:101, 1797). The specimens in these collections are cited by Ray and by Hudson.

Adam Buddle (d. 1715) was a clergyman, vicar of Cambridge in Sussex, and much interested in British plants. His *hortus siccus* is still among the collections of Herb. Sloane in the British Museum. James Petiver (1658–1718) was the apothecary to Charterhouse and his collection of plants is still in Herb. Sloane. Rev. Robert Uvedale (1642–1722) was vicar of Cambridge in Sussex and his herbarium constitutes volumes 302 to 315 of the Sloane collection of the British Museum. All were contemporaries of John Ray, who consulted their specimens and referred to them definitely by volume, page, and

number. Goodenough and Woodward, by their studies and their references to them, indicate the importance of these specimens in initiating the earlier ideas of algal species.

Dawson Turner (1775–1858) was a banker of Yarmouth. It is said that he was instructed as to marine algae by Mr. Lilly Wigg (1749–1828), who was well known to Woodward, to Goodenough, and to other botanists of his time and seems also to have merited the reputation of a keen and accurate observer. Turner, in correspondence with Mertens, with Roth, with Stackhouse, and with Esper, benefited by the work of Goodenough and of Woodward and established a sort of fixed tradition and this accounts for a tendency on the part of J. G. Agardh (1848, p. 340) and others to regard Turner's interpretation of Linnean names as "*sancta.*" Turner does refer to the specimens in the Linnean herbarium, but not as having examined them himself. Turner's great work was the Fuci sive plantarum Fucorum generi a botanicis ascriptarum icones descriptiones et historia (1808–1918), which is generally referred to as the "Historia Fucorum." An earlier work, A Synopsis of the British Fuci, (1802) in which Turner gives full information as to history, etc., is seldom quoted, although of very great importance since it also embodies much personal observation of moment. The Synopsis, which was at first intended to be little more than a republication of "Dr. Goodenough and Mr. Woodward's excellent paper in the third volume of the Linnean Society," was finally written entirely anew. Turner (Synopsis, p. viii) mentions that "the old Herbaria preserved in the British Museum are universally acknowledged to be of so much importance in the ascertaining several of Ray's, Morison's, and Hudson's species," and regrets never having seen them but quotes them and gives thanks to his friend, "Mr. Dillwyn, who took the trouble of examining them with care" on his account, besides borrowing from Goodenough and Woodward's paper. It might appear that at this time at least, Turner was not familiar with the specimens in the Linnean herbarium, since he seems to rely here largely upon the paper of Goodenough and Woodward. It is to be presumed that his remarks on Linnaean specimens in the *Fuci* may be at first hand, since he concerns himself also with Linnean types of non-British species.

Many phycologists are in the same situation as Mertens, Roth, Wulfen, and Esper, as regards the possibility of consulting the specimens of Linnaeus, of Buddle, of Uvedale, etc., but find themselves in a more favorable situation, as Turner did, because of the careful

and critical work of Goodenough and Woodward. It seems more and more evident from the various accounts that Goodenough and Woodward set the example for critical examination of the *Fuci* and this work was adopted and made of even more influence by Turner. Woodward (1797) also turned his attention to *Ulvae* (as then understood), while Lewis Weston Dillwyn (1778–1855), china manufacturer, member of Parliament, etc., monographed the British Confervae (1802-1807) (as then understood). Associated as a younger man, particularly with Dawson Turner (his father-in-law) and with Dillwyn, was William Jackson Hooker (1778–1855), through whom the inspiration descended to Joseph Dalton Hooker, William Henry Harvey, etc., to the generation more recently passed away.

This brief, but it is hoped suggestive sketch, relaying, as it were, the activities in algal nomenclatorial endeavor, from Morison, Buddle, Petiver, Uvedale, Ray, etc., through Hudson, to Goodenough, Woodward, and Dillwyn, to Dawson Turner, to be continued, so far at least as British algae were concerned, through William Jackson Hooker and Robert Kaye Greville, to Joseph Dalton Hooker and William Henry Harvey, may be regarded as introductory to the general phase of examination into the sources for all attempts to determine the exact status of many (or most?) of the earliest algal names. The fact that the Linnean Herbarium came to rest in London, where the "old herbaria" were also preserved, gave these British workers an overwhelming advantage which, led by Goodenough and Woodward, they used to their profit and that of the rest of the world interested in settling various questions basic to monographic work.

Codium tomentosum (Huds.) Stackh. has long been known under this name and any doubt cast upon the stability of this binomial is to be avoided if possible. The generic designation may not even yet seem finally settled, but there are ways still open for dealing with generic names. The specific name is derived from *Fucus tomentosus* Hudson, published in the second edition of the Flora Anglica in 1778 (p. 584). The usual reference from Turner (1811, pp. 1, 3) is to "F. Angl., p. 584," without date or edition being mentioned, but O. C. Schmidt (1923, p. 39) gives the date as 1797, the date of the third edition. Hudson's specimen does not seem to be available, at present, and it is not referred to by Goodenough and Woodward, hence further inquiry must be made as to Hudson's conception of his species. His description: "*Fucus fronde compressa dichotoma tomentosa obtusa,*" is not only not distinctive, but at least misleading,

through the use of the term "*compressa.*" Hudson's first citation: "elongatus. *Fucus fronde filiforme compressa dichotoma articulata, geniculis tumidiusculis.* Syst. nat. 716. Sp. Pl. 1627," evidently refers to the *Fucus elongatus* of Linnaeus, as published on p. 716 of the second volume ("Vegetabilia") of the twelfth edition of the Systema Naturae (1767) and earlier on p. 1627 in volume 2 of the second edition of the Species Plantarum (1763) where the description reads: "... *Elongatus. Fucus fronde filiforme compressa dichotoma recta.*" Linnaeus, however, proposed his *Fucus elongatus* on p. 1159 of the second volume of the first edition of the Species Plantarum (1753) with the description: "*Elongatus. Fucus fronde filiformi teretiuscula dichotoma recta geniculis tumidiusculis.*"

The quotation of the *Fucus elongatus* of Linnaeus, which is not only in the second edition of the Species Plantarum, but also in the first edition, suggests possibly that Hudson may have had some doubt as to the identity of his plant and that of Linnaeus, but he does not indicate that he has. The question remains, however, as to why he gave a new name to a plant which had already been named and described. There seems to be little doubt that the plant named *Fucus elongatus* by Linnaeus was an entirely different plant from that named *Fucus tomentosus* by Hudson. Goodenough and Woodward (1797, p. 196) and later writers excluded this Linnean reference to *F. elongatus* from the proper synonymy of *Fucus tomentosus* of Hudson and attached it to *Fucus loreus* Linnaeus, which will be discussed later.

To resume the references under *Fucus tomentosus* Hudson (1778, p. 584), the second reference reads: "*Fucus sponginosus teres ramosior viridis erectis.* Hist. Ox. III, 647, S. 15, t. 8, f. 7." This reference is to Robert Morison's Historiae Universalis Oxoniensis, already alluded to and the figure cited seems clearly that of the plant usually assigned under *Codium tomentosum.* The particular point to be noted here is the fact that Linnaeus, in both editions of the Species Plantarum, quotes this reference, including the figure of Morison, under his *Fucus elongatus.* It was this erroneous citation of Morison's figure by Linnaeus that, presumably, led Hudson to include *Fucus elongatus* under his *F. tomentosus.*

The third (and last) citation of Hudson, under his *Fucus tomentosus* reads: "*Spongia dichotomos teretifolia viridis.* R. syn. 29," which is from John Ray's synopsis methodica stirpium britannicarum, ed. 3, 1724 (p. 29 as quoted). Ray, in turn, also quotes the Morison reference (with figure) given above, so that this reference

also clearly points to the present *Codium tomentosum*. It seems therefore that the *Fucus tomentosus* of Hudson's second and third editions (p. 584, 1778, and p. 584, 1797) are certainly the plant now called *Codium tomentosum*, but excluding the cited synonym, *Fucus elongatus* L.

The question then arises as to whether this plant, seemingly well known to Hudson, may not have been included in the first edition (1762) of the Flora Anglica. Search fails to reveal a *Fucus tomentosus*, but following a suggestion from the inclusion under this species of the Ray and Morison references (given above), the same citations were found on page 489 under the binomial *Spongia dichotoma*. Since the first edition of the Flora Anglica seems unusual, at least in quotation, the statements of Hudson are reproduced here:

2. SPONGIA erecta dichotoma compressa *dichotoma*.

Spongia dichotomos teretifolia viridis. *R. syn.* 29.

Fucus spongiosus teres ramosior viridis erectis. Hist. Ox., III, 647, t. 8, f. 7.

Fucus filiformis compressus dichotomos rectus: geniculis tumidiusculis. *Sp. pl.* 1159.

Anglis, forked sponge.

Habitat in littoribus marinis. In Cornubia. R. Syn. in littore Eboracensi, sed rarius.

It will be seen on comparison that the citations under *Spongia dichotoma* are the same as under *Fucus tomentosus*, but the Ray citation is placed first, the Morison citation (with the figure) second, and the Linnean citation of *Fucus elongatus* (of the first, or 1753 edition, however, rather than of the second, or 1763 edition) is placed last. There can therefore be no doubt that the *Spongia dichotoma* Hudson (1762) is intended for the same species as that included under the *Fucus tomentosus* Hudson (1778). The binomial *Codium tomentosum* (Huds.) Stackh. therefore must yield to the new combination, **Codium dichotomum** (Huds.).

The confusion, or misapplication of names, unfortunately does not end with the necessary change of the old and familiar *Codium*. The early confusion over *Fucus elongatus* L. remains to be straightened out. There seems to be no doubt in the minds of all writers since the time of Goodenough and Woodward (1797), that Hudson was mistaken in citing this species under his *Fucus tomentosus* and, therefore, there can be no doubt that the citation under *Spongia dichotoma* was also erroneous. Goodenough and Woodward (1797, p. 178) deter-

mined that the type specimen of *Fucus elongatus* L., which is represented in the Linnean herbarium by a plant marked as the one published in the first (1753) edition of the Species Plantarum (*cf.* Benjamin Daydon Jackson, 1912, p. 77), is simply a portion of a plant of *Fucus loreus,* the breaking, or articulation, of the plant as described by Linnaeus being "merely the effect of drying after having been affixed to the paper." Since *Fucus elongatus* L. antedates *Fucus loreus* by somewhere about fourteen years, it is evident that the species name *elongata* is to be preferred and the species must be called **Himanthalia elongata** (L.) *comb. nov.,* instead of *Himanthalia lorea* (L.) Lyngb.

A second query, as to types, leads back also to the first edition of Hudson's Flora Anglica and the "old herbaria." This query is as to the type of *Gelidium corneum* (Huds.) Lamour. Lamouroux (1813, pp. 40, 41), in founding the genus *Gelidium,* mentions first *G. corneum,* citing *Fucus corneus* Turn. Hist. as the first species and presumably the type of the genus. Turner, both in the Synopsis (1802, 2:272–280) and in the *Fuci* (1819, p. 147) was so deeply impressed with the multiplicity of seemingly intergrading forms that he felt it necessary to refer them all to this species, and in this he reflected also the feeling of Goodenough and Woodward (1797, p. 183), although the latter realized the significance of the fact that the varieties they recognized grew in distant situations and so detached from one another that they ought to be separated as distinct species, but that their limits cannot be ascertained. Thuret and Bornet (Bornet et Thuret, 1876, p. 58), on the other hand, seem convinced not only that there are several species concerned but that they can be separated. Turner (1802, p. 280) calls attention to the fact that Linnaeus confounded the *Fucus corneus* Huds. with his *Fucus cartilagineus* (1753, p. 1161), but since Linnaeus has also specimens from the Cape under his species, it seems that it was that species which was intended rather than *F. corneus.* Linnaeus also gives the habitat as being in the southern seas. In attempting to determine typical *Fucus corneus* Huds., the attention of the writer was drawn to the fact (by Mr. A. Gepp, about 1912) that Hudson quotes Ray and Buddle, and an examination of the Buddle specimen in Herb. Sloane at the British Museum indicated that what seems very clearly to have been in Hudson's mind, in selecting the name "*corneus,*" was Buddle's description and plant. As Goodenough and Woodward (1797, p. 183) have stated: "the specimens preserved in Buddle are large, and being blanched, so

justly answer his description of *corneus et tenax,* that we preserve the name *corneus.*" They go on farther to say: "The propriety of this appellation is seen only in these larger and thicker specimens." To one who has seen the Buddle specimens and contrasted with them specimens of the other varieties referred to *Fucus corneus,* the inclination to regard the Buddle specimens as the type of *Fucus corneus* Hudson crystallizes into certainty as the investigation proceeds. It is certain that it is the only specimen cited and it answers the description of Hudson: "*Fucus cartilagineus, caule teretiusculo compresso ramosissimo ramis subpinnatis, laciniis acutis fructiferis.*" A photograph obtained through the kindness of the officials of the British Museum of Natural History is reproduced on plate 31. The Buddle specimen is the var. *sesquipedale* of Turner's account (1819, p. 146, pl. 257, f.), the *Gelidium sesquipedale* Thuret (see Bornet et Thuret, 1876, p. 61; Bornet, 1892, p. 271).

The determination of Hudson's *Fucus corneus,* as a distinct entity, is necessary to offset the idea of *Fucus corneus* Turner as represented on plate 257, figure 2, of the fourth volume of the Fuci (1819), an idea which has obscured the whole study and consideration of *Gelidium corneum,* until as a result, the species is assumed to be either too general and too polymorphic to be manageable or drops out of consideration entirely as in the treatment of *Gelidium* in De Toni's Sylloge Algarum. It is hoped that a later paper may discuss this matter further.

Fucus corneus Hudson is usually quoted as Flora Anglica, p. 585, which may be either from the second edition (1778) or the third (posthumous) edition (1797). It was proposed, however, in the first edition in 1762 (p. 474) which should be quoted to authenticate the publication of the species. As to just what was included by Hudson under *Fucus filicinus* (Flora Anglica, ed. 1, p. 473, 1762; ed. 2, p. 586, 1778) and *Fucus pinnatus* (Flora Anglica, ed. 1, p. 474, 1762; ed. 2, p. 586, 1778) is not clear, and may not become so unless Hudson's own specimens are discovered, since no specimens are quoted. Turner (1819, p. 146) identified the *F. filicinus* with the *F. corneus* var. ι of Goodenough and Woodward (1797, p. 182), apparently from specimens sent to Turner (1802, p. 278) by Dr. Goodenough. Turner (1819, p. 249) describes it as: "*fronde setacea; pinnis horizontalibus, dilatatis, obtusissimis,*" while Hudson's description (1762, p. 473) reads: "Fucus *cartilagineus compressus, frondibus supra-decompositis pinnatis, laciniis obtusis,*" and (1778, p. 586) "Fucus, *fronde carti-*

laginea compressa decomposito-pinnata, laciniis horizontalibus obtusis." Turner's reference (Turner, 1819, p. 149, pl. 257, fig. d) seems to be at least doubtful, since his plant has filiform (or setaceous) primary axes extending out into dilated lateral obtuse branches. *F. pinnatus* Hudson (Flora Anglica, ed. 1, p. 474, 1762) is described as: "Fucus *membranaceus, frondibus triplicato-pinnatis.*" Further discussion of Turner's conception of *Fucus corneus* and its varieties will be the concern of a later paper. At present the stabilization of the conception of Hudson and its relation to his ideas of *F. filicinum* and *F. pinnatus* are all that will be attempted.

Before leaving the matter of the earlier writers and the older herbaria, particularly the English, and the confusions then and now existing, it may be proper to refer to one of the puzzles in identity which remains unsolved. In 1797, Thomas Jenkinson Woodward, already alluded to in connection with Dr. Goodenough, published his: Observations upon the Generic Character of *Ulva,* with Descriptions of Some New Species. Woodward's conception of the genus, so broad and including so many discordant elements as were then referred to it, shows due appreciation of the unwieldy character of these earliest genera of Algae. The genus *Ulva* was primarily and typically made up of membranaceous Algae, such as species of the present-day genera of *Ulva* (as now limited), *Enteromorpha, Porphyra,* etc., but the character: "*Fructificationes in membrana vesiculari absque fronde,*" led to extensions, until the distinction between *Ulva* and *Fucus* came to be difficult. On this account, Woodward seems to have referred to the genus *Ulva,* a plant which he regarded as having an anomalous structure for *Ulva,* but not, however, as able to qualify as a *Fucus,* although from our later point of view he should have recognized its affinity to the *Fucus tomentosus* Hudson. This plant he named *Ulva decorticata* (Woodward, 1797, p. 55). No herbarium specimen can be traced at present, but Turner (1811, p. 4, *sub Fucus tomentosus* var. *elongatus*) speaks almost as if he had seen the specimen. It may be that Mr. Lilly Wigg, to whom the plant was given, along with other marine plants, by a sailor, retained the specimen and showed it to Turner. Turner very properly associates it with *Fucus tomentosus* and even makes it a variety of that species, but Woodward gives no hint in his discussion of the species that such a relationship suggested itself to him, nor do Goodenough and Woodward mention *Ulva decorticata* when discussing *Fucus tomentosus.* C. A. Agardh (1822, p. 454) proposed the binomial *Codium elongatum* for a plant from

Cadiz, referring the *Ulva decorticata* Woodward to it as a synonym. M. A. Howe (1911, p. 494) substituted *Codium decorticatum* (Woodward) Howe for C. *elongatum* Ag., and has since been followed. Doubts, however, have been growing as to the certainty of the identity of the two species. Recently, Boergesen (1925, pp. 95–97) has explained why he cannot agree to the views of Howe. The particularly striking points in the morphology of the plant as described by Woodward are its length and its branching. The length of the specimen is given as 6 feet and 6 inches, and the plant and the base described as expanded, so that in all probability the plant was complete. It was divided into three or four or more parts near the base. One of the parts was very short, two dichotomies divided about 6 inches above their origin and their divisions simple to the top, while the longest branch (or principal frond) continued simple for 3 feet, then forks into simple divisions. The ends of the branches were attenuate and terminate obtusely. The whole plant, when swollen up with water, was filiform, except that the branches were compressed at their origin and again above and below the angles of their dichotomy. It is compared with *Fucus loreus*. It is described as being four lines in diameter ("lata"), or about 8 mm. The length, in particular, is striking, and suggests relation to a more recently described species, *Codium Chazaliei* Weber-van Bosse (1899, p. 134) which resembles *Ulva decorticata* more closely in habit and size, and originated in the Cape Verde Islands, whence the sailor who brought Woodward's specimen to him, may possibly, without allowing unreasonable latitude for imagination, have obtained it. Such long plants are apt to be of deeper water rather than shore plants, and such are frequently dislodged by anchors and even brought up with them when they are raised and hoisted aboard. *Codium Chazaliei* is certainly different from *C. elongatum* Ag. As Boergesen (*loc. cit.*) and Setchell and Gardner (1930, pp. 130, 131) indicate, *C. decorticatum* is too uncertain in its application to supplant other binomials, until some happy chance may uncover the original specimen.

To summarize, the following synonymy becomes apparent from the foregoing considerations:

Codium dichotomum (Huds.) comb. nov.

Spongia dichotoma Hudson, Flora Anglica, ed. 1, p. 489, 1762.

Fucus tomentosus Hudson, Fl. Anglica, ed. 2, p. 584, 1778 (rejecting Syn. Linn.).

Codium tomentosum Stackhouse, Nereis Britannica, ed. 1, p. xxiv, 1797.

Himanthalia elongata (L.) comb. nov.

Fucus elongatus Linnaeus, Sp. Alg. (ed. 1), vol. 2, p. 1159, 1753 (rejecting syn. Moris.).

Fucus loreus Linnaeus, Syst. Nat., ed. 12, vol. 2 (Veg.), p. 716, 1767.

Himanthalia lorea Lyngbye, Hydr. Dan., p. 36, 1819.

Gelidium corneum (Huds.) Lamour. (in sens. strict.), Essai sur les gen. de la fam. des Thalass. non art., p. 41, 1813.

Fucus corneus Hudson, Flora Anglica, ed. 1, p. 474, 762.

Fucus corneus ι *sesquipedale* Clemente, *in* Turner, Fuci, vol. 4, p. 146, pl. 257, fig. f, 1819 (excluding other varieties).

Fucus parvus pennatus flavicans, corneus et tenax Buddle, Plantae Britannicae, vol. II, p. 2, no. 2, *in* Herb. Sloane, 114–116 (Brit. Mus. Nat. Hist.). (See plate 31 for reproduction.)

Gelidium sesquipedale Thuret, *in* Bornet et Thuret, Notes Algologiques, p. 61, 1876.

LITERATURE CITED

AGARDH, C. A.
1822. Species Algarum, voluminis primi, pars posterior.

BOERGESEN, F.
1925. Marine algae from the Canary Islands. I. Chlorophyceae.

BORNET, M. EDOUARD.
1892. Les algues des P. K. A. Schousboe, etc. Mem. Soc. Nat. Sci. Nat. Cherbourg, **28**:165–376, pl. 1–3.

BORNET, MM. ED. et G. THURET.
1876. Notes algologiques, Fasc. I.

BUDDLE, ADAM.
Plantae Britannicae, vols. 1–3, *in* Herb. Sloane, 114–116, *in* British Mus. Nat. Hist., London (*Hortus siccus*).

GMELIN, SAMUEL GOTTLIEB.
1768. Historia Fucorum.

GOODENOUGH (REV. SAMUEL) and THOMAS JENKINSON WOODWARD.
1797. Observations on the British Fuci, with particular descriptions of each species. Trans. Linn. Soc. London, **3**:84–235, pl. 16–19 (read April 7, 1795).

HOWE, MARSHALL AVERY.
1911. Phycological Studies. V. Some marine algae of Lower California. Bull. Torr. Bot. Club, **38**:489–514, pls. 27–34.

HUDSON, GULIELMUS (WILLIAM).
1762. Flora Anglica, ed. 1.
1778. Flora Anglica, ed. 2.
1797. Flora Anglica, ed. 3 (posthumous).

JACKSON, BENJAMIN DAYDON.
1912. Index to the Linnean herbarium, etc. Suppl. Proc. Linn. Soc. London for the 124th session.

LAMOUROUX.
1813. Essai sur les genres de la famille des Thalassiophytes non articulées.

LINNAEUS, CAROLUS.
1753. Species Plantarum (ed. 1).
1762. Species Plantarum, vol. 1 (ed. 2).
1763. Species Plantarum, vol. 2 (ed. 2).
1767. Systema naturae. Editio duodecima, reformata. Tomus II (Vegetabilia).

MORISON, ROBERT.
1715. Plantarum Historiae Universalis Oxoniensis seu herbarum distributio, nova, etc. Vol. 3.

RAIUS, JOANNES (JOHN RAY).
1724. Synopsis methodica stirpium britannicarum, ed. 3.

Schmidt, Otto Christian.
1923. Beiträge zur Kenntniss der Gattung Codium. Bibloth. Bot., Heft 91.

Setchell, William Albert, and Nathaniel Lyon Gardner.
1920. The Marine Algae of the Pacific Coast of North America. Part II, Chlorophyceae. Univ. Calif. Publ. Bot., 8:139–374.
1930. Marine Algae of the Revillagigedo Expedition in 1925. Proc. Calif. Acad. Sci., ser. 4, 19:109–215, pl. 4–15.

Stackhouse, J.
1795–1801. Nereis Britannica, etc. (ed. 1):
Fasc. 1, pp. I–VIII, 1795.
Fasc. 2, pp. IX–XXXII, 1797.
Fasc. 3, pp. XXXIII–XL, 1–112, app. 4 pp., index, etc., 3 pp., pl. 1–17 (and A–G), 1801.

Turner, Dawson.
1802. A synopsis of the British Fuci, vols. 1, 2.
1811. Fuci sive plantarum fucorum generi a botanicis ascriptarum icones, descriptiones et historia, vol. 3.
1819. *Ibid.*, vol. 4.

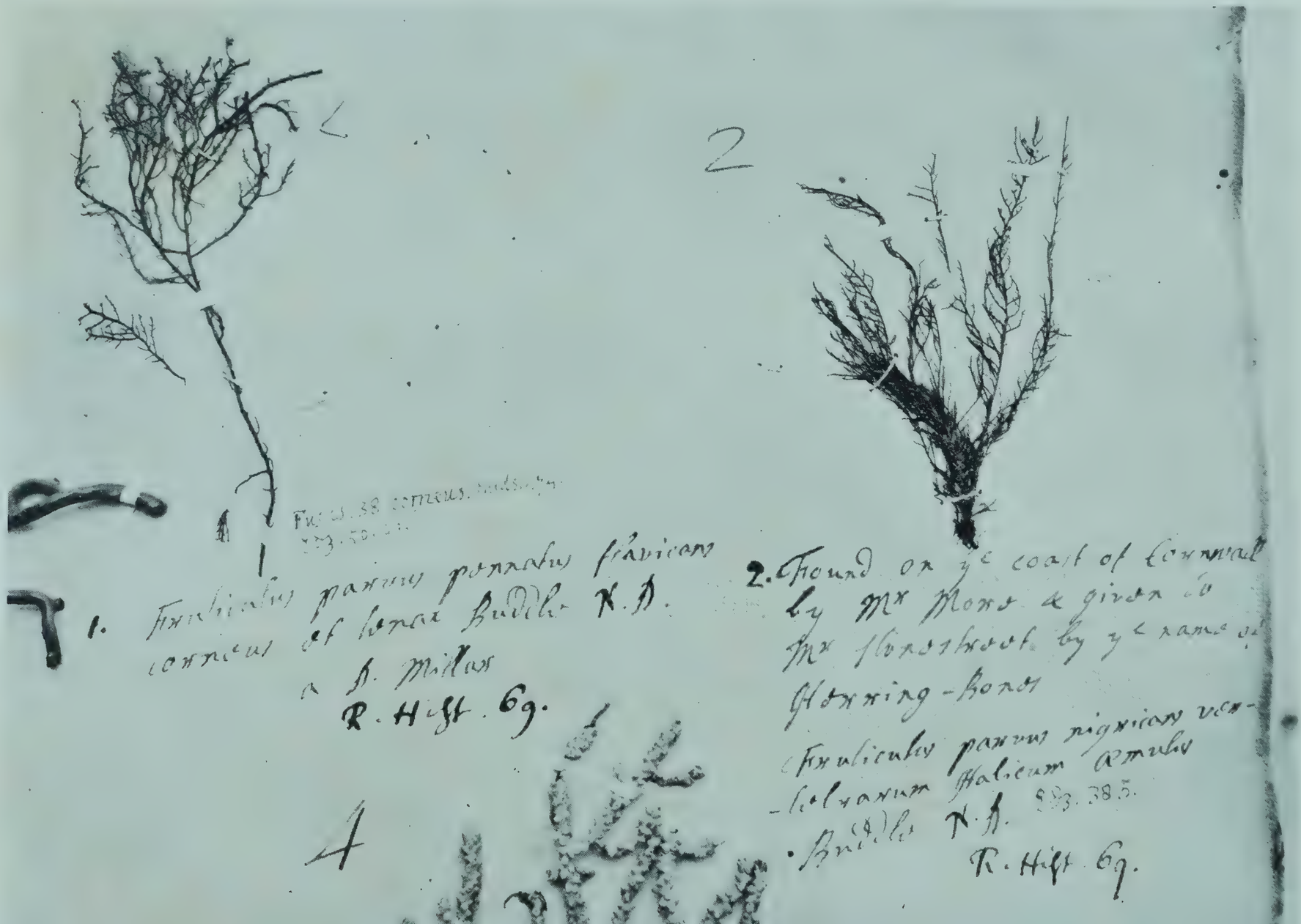
Weber-van Bosse, Mme. A.
1899. Note sur quelques algues rapportées par le Yacht "Chazalie." Jour. de bot., 13:133–135.

Woodward, Thomas Jenkinson.
1797. Observations upon the generic characters of *Ulva*, with descriptions of some new species. Trans. Linn. Soc., London, 3:46–58 (read Dec. 2, 1794).

EXPLANATION OF PLATE

PLATE 31

Portion of sheet in Adam Buddle's *Plantae Britannicae*, vol. II, p. 2, no. 2. showing "*Fucus corneus* Huds." and adjoining specimens. × 16/17 diam.


1
2
4
1. Fruticulus parvus ramosus fragilicans corneus ad littora Buddle N.H.
a H. Miller
R. Hist. 69.
2. Found on ye coast of Cornwall by Mr Moore & given to Mr Hanstreet by ye name of Herring-bone
Fruticulus parvus nigricans ramulis Halicum æmulus
Buddle N.H.
R. Hist. 69.

STUDIES IN PENSTEMON

BY

DAVID D. KECK

University of California Publications in Botany
Volume 16, No. 11, pp. 367–426, 18 figures in text
Issued February 11, 1932

University of California Press
Berkeley, California

Cambridge University Press
London, England

STUDIES IN PENSTEMON*

A SYSTEMATIC TREATMENT OF THE SECTION SACCANTHERA

BY

DAVID D. KECK

The large genus *Penstemon,* of the *Scrophulariaceae,* has been chosen for study partly because of the interest aroused in it by workers in the fields of genetics, cytology, and ecology, as well as that of taxonomy; and partly because of its peculiar fitness for taxonomic investigation by experimental methods. This fitness is manifest in its availability, the center of distribution being in the western United States; in its adaptability, as it is possible to grow numerous members in the garden from transplants, cuttings, and seeds; and in the possibility of unlimited study of abundant unsolved taxonomic problems. The genus is of further interest because of its horticultural value, additional species finding their way into seedsmen's lists yearly. The investigations are being taken up section by section. The present paper represents results obtained in the section *Saccanthera,* the first to be studied in this connection.

The first concern of a worker studying plant materials in most lines of botany is with regard to identification of the forms at hand. His second thought is of the identity of the nearest relatives of his material, or the relationships of his plants. It is the function of the taxonomist to present this necessary information as the basis for work in the allied fields of botany. Hence it is hoped that the ultimate monograph of this genus will be of utility to others not only as a classification of the species and their recognizable segregates, with an indication of their probable evolutionary origins, but also for explanations as to the reasoning employed, and statements as to the existence of forms that can not be accorded nomenclatorial recognition at present.

---

* Name proposed by Mitchell (Act. Phys. Med. Acad. Nat. Cur. 8: App. 214, 1748) prior to the beginning date for genera. Linnaeus failed to recognize the new genus, referring its species to *Chelone.* Name again proposed by Mitchell (Dissertatio 36, 1769). Orthography "Pentstemon" preponderant in literature although not proposed until 1789. Pennell (Contr. U. S. Nat. Herb. 20: 325, 1920) returned to original spelling and has been followed by all subsequent workers making revisions within the genus. Sprague (Kew Bull. Misc. Inf. 359, 1928) interprets original spelling as the one to follow. Either spelling is incorrect Greek.

Methods and Materials

The present investigations have employed experimental, field, and herbarium methods of study.

The experimental phase has included the garden-growing of sixteen of the nineteen species. Members of the sixteen species were dug as transplants and moved into the gardens. For some species the roots were divided, forming clones of the individuals. Propagules from a single plant were then grown in as many as nine different gardens, representing nine sets of ecologic conditions, distributed between three different altitudes. Such treatment has given definite answers to queries concerning, on the one hand, the fixity of characters, or, on the other, their ephemeral nature. As the characters examined are those used as criteria in classification, which in turn are often based upon relatively minute characters, these definite experimental results have proved invaluable. Only the more critical forms were subjected to the detailed treatment indicated. Some of the species died out before valuable results were obtained, but these were all regrown from seed collected with the roots. This practice has been avoided as far as possible in order to eliminate the unknown factors that enter with open pollination. Cooperative studies have been undertaken with Dr. C. W. Penland, of Colorado College, who is testing similar characters by the typical genetic procedure of studying the offspring of controlled pollinations. His work to date has not dealt with any species of this section, so the present paper does not touch upon it.

Field work has been carried on in most of the western states and sixteen of the nineteen species admitted to this section have been carefully studied in their native habitats. In many cases the flower measurements were made on this fresh material. These field studies yielded not only accurate notes on the living plant and information as to the flower-colors, too often entirely lost in drying, but also an opportunity to observe the general environment of each species. The latter is of much importance to one who would stress geographic distribution. Moreover, field studies permitted observations on the operation of such ecologic factors as local edaphic conditions, insect relations, and disease, together with their results as manifested by the degree of variation.

The herbarium studies were begun upon the collections of the University of California, which are the most extensive of the members of this section and which consequently have furnished the basis for most

of the detailed work here reported. Such an abundance of material has been available that citations of the better known species have been limited in this paper to representative collections that will picture the distribution of the species and, where there is a choice, the more widely distributed sets have been cited. The attempt has been made to cite specimens in geographical succession from east to west and from north to south. Likewise, descriptions have been abbreviated to the salient points that distinguish a species from its closest group of relatives within the section, except that in the case of new or little understood species these have been elaborated.

Supplementing the investigations in the Herbarium of the University of California (UC), the collections in the following herbaria were studied, the initials in parentheses being those used in citation:

Herbarium of the California Academy of Sciences (CA)
The working collection of the Carnegie Institution of Washington (CI)
Dudley Herbarium of Stanford University (DS)
Gray Herbarium of Harvard University (G)
Herbarium of Professor W. L. Jepson (Jepson)
Pomona College Herbarium (Po)
Rocky Mountain Herbarium of the University of Wyoming (RM)
Herbarium of the University of Oregon (UO)

Duplicates of my own collections have been sent to the herbaria of the following institutions as well as to several of those mentioned above:

Botanical Museum and Gardens, Berlin (Berlin)
Botanical Conservatory, Geneva (Geneva)
Royal Botanic Gardens, Kew (Kew)
Missouri Botanical Gardens (Miss)
New York Botanical Garden (NY)
The Academy of Natural Sciences of Philadelphia (Phila)

My best thanks are due to those in charge of all the above-named herbaria and to many others who have rendered various courtesies. The actual work has been carried out in connection with a project of the Carnegie Institution of Washington, this project having as its goal a comprehensive study of the entire genus. My thanks are therefore due also to Dr. H. M. Hall who, as member in charge of the work in experimental taxonomy, has encouraged the study at all stages. Finally, it is a pleasure to acknowledge much helpful advice from Dr. W. L. Jepson, to whom the text of this paper, in a somewhat different form, was presented in partial fulfillment of the requirements for the degree of doctor of philosophy at the University of California.

The Section Saccanthera

The section *Saccanthera* was proposed by Bentham[1] in 1846. This was accepted by subsequent botanists without modification until 1906 when Rydberg[2] segregated from it the species-group *Bridgesiani* for the single species *Penstemon bridgesii* Gray. In 1917, Rydberg[3] retained this new group and divided the remaining species of Bentham's *Saccanthera,* so far as they came under the scope of his treatment, into the species-groups *Glandulosi* and *Azurei.* The last-named included all but the single species *P. glandulosus* Lindl. Pennell,[4] in his treatment of the Rocky Mountain members of the genus, used the sectional names *Bridgesiani* and *Heterophylli* for this material. In the present paper, Pennell's arrangement has been followed, with the *Heterophylli* including all the species of *Saccanthera* excepting *P. bridgesii* Gray. *Bridgesiani* and *Heterophylli* have been reduced to subsections but are not relegated to synonymy under the one name *Saccanthera,* because the origin of *P. bridgesii* seems to be plainly in the section *Elmigera* Benth., while that of the other species of *Saccanthera* appears to be in the section *Graciles* Pennell.

The Subsection Bridgesiani

The type species is the only one admitted under the subsection *Bridgesiani. Penstemon bridgesii* appears very certainly to be more closely related to members of the section *Elmigera* than to the other species of *Saccanthera.* It probably originated from such a species as *P. barbatus* of *Elmigera* with which it agrees in flower-color, reflexion of the lower lip, with accompanying extension of the upper lip, and a tubular corolla with pubescence in the throat. These characters also serve to separate *P. bridgesii* from other species of *Saccanthera.* In addition, the geographical distribution of *P. bridgesii* links it with members of section *Elmigera,* rather than those of section *Saccanthera.* The saccate anther, peculiar to the latter section, links the subsections *Bridgesiani* and *Heterophylli,* but slight differences in the form of this organ in the two subsections indicate a possibility of separate origins. It seems unwise, however, to go one step farther and erect a section for this species, as *P bridgesii* bears a slight resemblance to *P. gracilentus, P. caesius,* and *P. scapoides,* of the subsection *Heterophylli,* in

[1] DC. Prodr. 10:329, 1846.
[2] Fl. Colo. 308, 1906.
[3] Fl. Rocky Mount. 767, 1917.
[4] Contr. U. S. Nat. Herb. 20:335, 1920.

habit, corolla, and pubescence that should not be entirely overlooked. *Penstemon bridgesii* has become well separated from its nearest known relatives and may have had an early origin, in fact, one as early as any other species of the section *Saccanthera.*

The Subsection Heterophylli

On a basis of origins, three groups may be made of the species in the subsection *Heterophylli.* These appear to have arisen separately within the section *Graciles* of Pennell (*l. c.* 326). That is, each of the three groups appears to present a more definite connection with a species of section *Graciles* than with any species of section *Saccanthera.* This, based upon comparative morphology of present-day species, is a translation of past evolutionary activity of which only the present-day results are available. It is possible that, were we able to read the past, these three groups of subsection *Heterophylli* would merge, being entirely homogeneous at the time of origin. But based upon the results as known, it is to be assumed that subsection *Heterophylli* had its inception within *Graciles* at an earlier time than any of its species actually appeared, so that the potentiality for producing saccate anthers (the key character of section *Saccanthera*) was distributed among a few closely related species of *Graciles.* Then when the creation of species bearing saccate anthers was accomplished, three species, the forerunners of independent lines, appeared from separate though closely allied sources within *Graciles.* In other words, the focal point of these three lines, instead of being on the horizon is just below the horizon, so that it could scarcely be said that we were dealing with polyphyletic origins.

The first group, in the order of this treatment, is composed of *P. gracilentus, P. caesius,* and *P. scapoides.* Each of these species is well set off from any other, the two last being more closely related to each other than to *P. gracilentus.* The saccate anther is the main character of importance by which *P. gracilentus* is separated from such a species as *P. procerus* of *Graciles,* and it is logical to assign its origin to the *P. procerus* group.

The second group is the largest and the evidence points to its origin in the general region of southern Idaho and northern Nevada. *Penstemon cusickii* is taken to be the most primitive species and it is closely connected with *P. humilis* in the broad sense. One short evolutionary branch from this primitive center includes *P. leonardii,*

P. platyphyllus, and *P. sepalulus,* Utah species that become progressively more glabrous as their relationship with *P. cusickii* is farther removed. The other line of development from the locus of *P. cusickii* includes most of the California members of the section. The Nevadan *Penstemon kingii,* placed next to *P. cusickii,* is intermediate between the latter and these Californian species both in morphological characters and geographical distribution. It is possible that the more specialized species of this subsection were connected with *Graciles* by intermediate forms of which *P. cusickii* and *P. kingii* are the modern representatives. This would rationalize the placing of the latter species of restricted distribution and numbers toward the base of a long line of complex species. The peculiar distribution of *P. kingii,* as well as some morphological heterogeneity, suggests, however, that it at least is better considered as a relict. The connection between *P. kingii* and *P. laetus* appears to be very close through subspecies *roezlii* of the latter. Within *P. laetus* there has been much change in the shape of the anther and the relative amount of dehiscence in that organ. The subspecies *typicus* has a large anther, dehiscent but little more than half the length of the sacs. The development of *P. azureus* is traced from this subspecies. *Penstemon laetus* subsp. *sagitattus,* with very narrow anthers dehiscent up to four-fifths the length of their sacs, is possibly the ancestral form from which P. *purpusii* and *P. heterophyllus* have been derived, species characterized by such anthers. The most interesting species of the group is *P. neotericus,* which apparently has arisen through hybridization of *P. laetus* with *P. azureus,* and apparently is as yet composed of just those characters received from these two parents.

In the northwestern United States there are five species of *Heterophylli* that constitute a group by themselves. All have sharply serrate or lobed leaves and a bearded sterile filament, which characters serve to separate them from the more southern species of the section. The only entire-leaved species with bearded sterile filaments are *P. gracilentus* and *P. scapoides,* neither of which has an obvious connection with these northwestern species. The probable origin of the five species appears to be in the section *Graciles,* as was the case with the other groups in the subsection *Heterophylli. Penstemon ovatus* of *Graciles* superficially resembles *P. diffusus* of *Heterophylli* closely, and analysis of the common characters supports the assumption of a near relationship existing between them. *Penstemon pruinosus* of *Graciles* differs from these in minor characters. As no other species of the five can

show so obvious a connection with another species outside of its group, even within its section, *P. diffusus* is considered the primitive member of the group. Accepting *P. diffusus* as the starting point, it is seen to lead to *P. glandulosus* by one line of development, to *P. venustus* by another, and to *P. richardsonii* by a third. Apparently both *P. glandulosus* and *P. venustus* terminate their short branches of evolution, while *P. richardsonii,* a much more variable species, has evidently led to *P. triphyllus.*

Amplification of this synopsis of the probable course of evolution is given species by species.

The most critical organ in this section is the anther! Its method of dehiscence is the principal character that determines what species are admitted to the section, and it is the organ most frequently employed for the distinction of species within the section. But the small size of its parts often makes the general use of measurements unsatisfactory. Descriptions of the more subtle morphologic differences are difficult because of the variability that must be considered. Illustrations unfortunately show only one case out of many and are here given of typical forms with the suggestion that sufficient latitude in interpretation attend their use. The comparative sizes of this organ are variable in all species, and presence or absence of pubescence on the anther near its junction with the filament is inconstant in some cases.

Key to the Subsections and Species

I. Corolla scarlet-red, the throat nearly tubular; limb ⅓ or more the length of tubular portion; upper lip erect, the lower recurved from base.
Subsection I. **Bridgesiani**

II. Corolla blue, pink, violet, or purple, the throat dilated (practically tubular in no. 2); limb usually less than ⅓ the length of tubular portion; both lips usually recurving moderately.....Subsection II. **Heterophylli**

Subsection I. BRIDGESIANI

A single species.....1. **Penstemon bridgesii**

Subsection II. HETEROPHYLLI

A. Leaves entire (rarely toothed in no. 14); sterile filament glabrous (bearded in nos. 2 and 4).

B. Sterile filament bearded (glabrous in no. 3); leaves mostly basal; orifice of corolla bearded ventrally; throat prominently plicate ventrally; throat and tube indistinctly differentiated.

C. Flowers mostly fasciculate; corolla 13–16 mm. long; blades of basal leaves oblanceolate to narrowly spatulate, the petioles half as long; not caespitose .....2. **P. gracilentus**

CC. Flowers not fasciculate; corolla 17–35 mm. long; blades of basal leaves rotund, the petioles once or twice as long; caespitose.

D. Basal leaves glabrous; corolla 17–23 mm. long; orifice, but not throat, bearded ventrally; sterile filament glabrous. 3. **P. caesius**

DD. Basal leaves canescent; corolla 27–35 mm. long; orifice and throat bearded ventrally; sterile filament bearded.....4. **P. scapoides**

BB. Sterile filament glabrous; leaves well distributed; orifice of corolla glabrous; throat very moderately plicate or smooth; throat and tube usually distinctly differentiated.

E. Anthers purple-black, dehiscent for less than ½ the length of cells, the teeth on line of dehiscence minute. Great Basin area.

F. Corolla glabrous; calyx and summit of pedicel without stipitate clavate glands; anthers 1.2–2.1 mm. long.

G. Leaves puberulent; summit of pedicels usually puberulent. 5. **P. cusickii**

GG. Leaves glabrous; summit of pedicels not puberulent.

H. Sepals lanceolate to ovate, acuminate or sometimes acute; calyx 3.5–5.5 mm. long; stems puberulent; summit of pedicels glandular; plants not blue-glaucous.

I. Corolla 15–18 mm. long, the lobes deep blue, the throat violet-blue, the tube violet; anthers retuse at apex, sometimes merely truncate or rounded, 1.1–1.35 mm. long; stem-leaves mostly oblanceolate....6. **P. leonardii**

II. Corolla 22–25 (–30) mm. long, the lobes, throat, and tube lavender or violet; anthers obtuse or rounded at apex, 1.6–2.1 mm. long; stem-leaves mostly elliptic. 7. **P. platyphyllus**

HH. Sepals obovate or widely oblong, truncate at tip except for a small mucro; calyx 1.8–3.2 mm. long; stems glabrous; summit of pedicels glabrous; plants blue-glaucous. 8. **P. sepalulus**

FF. Corolla glandular-pubescent; calyx and summit of pedicel bearing stipitate clavate glands; anthers 1.1–1.2 mm. long....9. **P. kingii**

EE. Anthers buff to purplish, dehiscent for ½–⅘ the length of cells, the teeth on line of dehiscence prominent. California and adjacent areas.

J. Basal leaves narrowly oblanceolate to obovate, with short, petiole-like bases, always entire; herbage glabrous to finely pubescent.

K. Inflorescence glandular-pubescent; peduncles divergent from main axis.

L. Herbage not blue-glaucous, finely pubescent (rarely glabrate) below inflorescence; corolla blue-purple. 10. **P. laetus**

LL. Herbage blue-glaucous, glabrous below inflorescence; corolla usually tri-colored.....11. **P. neotericus**

KK. Inflorescence not glandular-pubescent (although sometimes puberulent); peduncles appressed to main axis.

M. Leaves just below inflorescence noticeably widest or flaring at base, amplexicaule; herbage below inflorescence glabrous, blue-glaucous.....12. **P. azureus**

MM. Leaves just below inflorescence not noticeably widest at base, sessile; herbage below inflorescence puberulent or glabrous, seldom blue-glaucous.....13. **P. heterophyllus**

JJ. Basal leaves with blade oval to rotund, the petiole half as long, sometimes serrulate; herbage densely canescent below inflorescence.....14. **P. purpusii**

AA. Leaves serrulate to parted; sterile filament bearded (glabrous in no. 19).

N. Plant not glandular-pubescent below inflorescence; sterile filament more or less bearded at tip; mature capsule exceeding sepals.

O. Inflorescence glabrous or puberulent but never glandular; sterile filament included.

P. Fertile filaments glabrous; leaves dimorphous, the basal petiolate, the upper cauline clasping; corolla 16–23 mm. long, the lobes not ciliate; calyx puberulent without, 6–11 mm. long.
15. **P. diffusus**

PP. Fertile filaments bearded above; leaves of one kind, all sessile; corolla 20–32 mm. long, the lobes ciliate; calyx glabrous without, 3–6 mm. long.....16. **P. venustus**

OO. Inflorescence glandular-pubescent; sterile filament exserted.

Q. Corolla (15–) 18–30 mm. long, pinkish, the lobes cleft ¼–⅓ the length of upper lip; leaves narrowly lanceolate to narrowly ovate in outline, 8–20 mm. wide; anthers 1.3–1.8 mm. long.
17. **P. richardsonii**

QQ. Corolla 12–15 (–19) mm. long, bluish, the lobes cleft ⅔ or more the length of upper lip; leaves linear to lanceolate in outline, 1–8 (rarely –17) mm. wide; anthers 0.9–1.2 (–1.3) mm. long.
18. **P triphyllus**

NN. Plant glandular-pubescent throughout; sterile filament glabrous; mature capsule exceeded by sepals.....19. **P. glandulosus**

I. Subsection **Bridgesiani** (Pennell) Keck comb. nov.

Penstemon (group) *Bridgesiani* Rydb., Fl. Colo. 306, 1906. *Penstemon* section *Bridgesiani* Pennell, Contr. U. S. Nat. Herb. 20:327, 1920.

Corolla scarlet-red, tubular; lips ⅓ or more the length of tubular portion, the upper erect, its lobes separated by a mere notch, the lower reflexed from base, its lobes parted ⅔ the way to base and spreading.

1. **Penstemon bridgesii** Gray



Fig. 1. *P. bridgesii* Gray. Anther × 10.

Penstemon rostriflorus Kellogg, Proc. Calif. Acad. 2:15, 1863. The original description, apparently a mixture compiled from two distinct species, does not apply accurately to this plant, and there is no mention of a type. Mrs. Curran (Bull. Calif. Acad. 1:145, 1885) examined a specimen that she took for the type

and pronounced it to be *P. bridgesii.* Because of the confusion and possibility of error surrounding this older name it is unwise to substitute it for the well-known *bridgesii.*

Penstemon bridgesii Gray, Proc. Am. Acad. 7:379, 1868.

Penstemon bridgesii rostriflorus Schelle, Handb. Laubh. Benen. 432, 1903.

Penstemon bridgesii var. *amplexicaulis* Monnet, Bull. Soc. Bot. France 61:228, 1914. According to the original description, the upper leaves are auriculate and amplexicaul. Type (*Monnet* 1036) from Gold Mountain (Esmeralda County), Nevada, has not been seen. A search on Gold Mountain by this writer did not disclose the species there. None of the material studied matches Monnet's description, so the variety should perhaps be retained.

Rather frequent on the less arid slopes of the upper Sonoran and Transition zones from southwestern Colorado, through southern Utah, northern Arizona, and southern Nevada into the Sierra Nevada of California from Mono County to the Mexican border. Rare in northern Lower California. "No. 218 in Californian collection of the late Thomas Bridges."

COLORADO. Montezuma County: Sierra el Late, *Brandegee* 1293 (UC). UTAH. San Juan County (?): Elk Ranch, *Jones* 6039*k* (Po). Wayne County: Juke's Butte, Henry Mountains, *Jones* 5664 (Po, RM). Piute County: near Marysvale, *Keck* 654 (CI, DS, Phila, Po). Washington County: Rockville, May 19, 1894, *Jones* (UC). ARIZONA. Coconino County: Flagstaff, *MacDougal* 267 (G, RM, UC); Fairview, *Jones* 4093 (CA, DS, RM, UC). NEVADA. White Pine County: Ward Mountain, July 6, 1928, *Jaeger* (CI, DS). Nye County: Currant, 1916, *Bentley* (DS, Po). Mineral County: Mount Grant, *Heller* 10907 (UC, G, DS). Clark County: Lee Canyon, Charleston Mountains, *Heller* 11000 (DS, G, UC). CALIFORNIA. *Bridges* 218 (G, type; isotypes DS, UC). Mono County: near Tioga, *Eastwood* 592 (CA). Tuolumne County: below Harden Lake, *Keck* 277 (CI, Po, UC). Fresno County: Collins Meadow, *Hall & Chandler* 356*a* (DS, UC). Kern County: Greenhorn Mountains, *Hall* 12976 (CI). Ventura County: Mount Frazier, *Elmer* 3747 (CA, DS, G, UC). Los Angeles County: Lytle Creek, *Johnston* 1557 (DS, Po, UC).

LOWER CALIFORNIA: Hanson's Ranch, July 26, 1883, *Orcutt* (UC).

A collection from Nellie, Palomar Mountain, San Diego County, California, *Valentian* 135 (UC), is doubtless a hybrid between this species and *P. heterophyllus* (see Hall, Univ. Calif. Publ. Bot. 6:169, 1915).

II. Subsection **Heterophylli** (Pennell) Keck comb. nov.

Penstemon (group) *Glandulosi* Rydb., Fl. Rocky Mount. 764, 1917; type species *P. glandulosus* Dougl. *Penstemon* (group) *Azurei* Rydb., l. c.; type species *P. azureus* Benth. *Penstemon* section *Heterophylli* Pennell, l. c.; type species *P. heterophyllus* Lindl.

Corolla bluish to purplish, usually with dilated throat; lips usually less than ⅓ length of tubular portion, both reflexed moderately.

2. **Penstemon gracilentus** Gray

Penstemon gracilentus Gray, Pacif. Rail. Rep. 6:82, 1857.

Perennial herb 2–7 dm. high: herbage bright green, seldom slightly glaucous, glabrous below inflorescence: leaves all of one kind or nearly so, more crowded at base of stems, linear-lanceolate to oblanceolate or spatulate, 2–10 cm. long, 2–18 mm. wide; the basal mostly with petiole half as long as blade: inflorescence a more or less compact panicle or thyrse; the flowers often in fascicles: corolla purplish blue, lavender-purple, or red-purple, 13–16 mm. long, 4–5 mm. wide at summit of throat, white-pubescent within orifice ventrally and on base of lower lip; upper lip recurving moderately, *ca.* 4.5 mm. long: lower pair of stamens extending into limb, upper pair nearly as long; the sterile filament bearded with yellow hairs for 4–5 mm.; the anthers black-purple, dehiscent less than half the length of sacs.



Fig. 2. *P. gracilentus* Gray. Anther × 10.

Rather common in good soils in the northern Sierra Nevada of California, especially on the eastern slope, from Siskiyou and Modoc counties to Placer County, and also in adjacent regions in Nevada, occurring at elevations of 1600–2900 m. "At the base of Lassen's butte, N. California." Type collected by Newberry.

NEVADA. Washoe County: Slide Mountain, *Heller* 10953 (DS, G, UC). Ormsby County: Fall Creek, *Baker* 1326 (CA, G, Po, RM, UC). CALIFORNIA. Siskiyou County: Medicine Lake, *Heller* 13691 (DS, Po); Mount Shasta, *Keck* 305 (CI, DS, G, Kew, UC). Shasta County: Hat Creek of Pit River, *Newberry* (G, type. This is "at the base of Lassen's butte," as stated by Gray, and is the only specimen in the Gray Herbarium that could be the type). Lassen County: Pine Creek, July 12, 1894, *Baker & Nutting* (DS, RM, UC). Plumas County: Prattville, *Keck* 968 (CI, DS, Phila, Po). Sierra County: Yuba Pass, *Smith* 2446 (CI, DS, G, Kew, Po, UC). Nevada County: Donner Lake, *Heller* 6958 (DS, G, Po, RM, UC).

This species is quite well separated from the other members of the section. In morphology of the anther, a character of importance and stability in this subsection, *P. gracilentus* stands with *P. cusickii, P. leonardii,* and *P. kingii.* Its habit and corolla are affiliated more closely with those of the *P. procerus* group of species in the section *Graciles.* In addition it is allied to *P. procerus* in color of herbage, glabrous leaves, frequently fascicled inflorescence, color as well as

shape of corolla, and bearded sterile filament. On the basis of the quantity of evidence at hand, it seems more natural to associate *P. gracilentus* with *P. procerus* and its segregates than with the above-mentioned species of the subsection *Heterophylli.* The anther of *P. gracilentus,* if dehiscent to the base, and allowed to gape wider as a result of a less extensive union of the two cells, would be a good match for those of several species of the section *Graciles.*

3. **Penstemon caesius** Gray

Penstemon caesius Gray, Proc. Am. Acad. 19:92, 1883.

Perennial herb 1.5–4.5 dm. high, loosely caespitose: herbage yellow- or blue-green, gray-glaucous, glabrous below inflorescence: leaves of two kinds, mostly basal; the basal with rotund blade 7–22 mm. long and narrow petiole of similar length; the upper cauline in 1 or 2 pairs, oblanceolate, subpetiolate or sessile: inflorescence an open panicle; the flowers never in fascicles: corolla purplish blue, 17–23 mm. long, 4.5–6.5 mm. wide at summit of throat, yellow-pubescent within orifice ventrally and on base of lower lip; upper lip erect, *ca.* 3 mm. long: lower pair of stamens ⅔ as long as corolla, upper pair nearly as long; the sterile filament glabrous; the anthers yellowish, dehiscent *ca.* ½ the length of sacs.



Fig. 3. *P. caesius* Gray. Anther × 10.

Frequent in the southern Sierra Nevada and the San Gabriel and San Bernardino Mountains of southern California, on dry, rocky slopes from 2000–3100 m. altitude. "S. E. California, on rocks in the San Bernardino Mountains, coll. Parry & Lemmon (1876, no. 304)."

CALIFORNIA. Fresno County: Dougherty Creek, Kings River, July 29, 1910, *Clemens* (Po). Tulare County: Salmon Creek, *Hall & Babcock* 5104 (UC, DS, RM). San Bernardino County: San Bernardino Mountains: near Fish Camp, *Johnston* 2842 (Po, RM); Bear Valley, *Parish* 462 (G, cotype); Sugarloaf Mountain, *Hall* 7529 (DS, Po, RM, UC); Mount Grayback, June 1880, *Wright* (G, cotype); labelled without definite locality, *Parry & Lemmon* 304 (G, type). Munz and Johnston (1924) cite the species from the San Gabriel Mountains.

This species is well separated from all others and does not seem to be a direct derivative of any present-day form. A case for its relationship with *P. kingii, P. laetus,* or *P. bridgesii,* based upon the similarity

of the glandular inflorescence, size of flower, shape of sepals and anthers, appears futile when the remaining characters are considered. If these were the only possibilities in the flora it would probably be most logical to consider *P. caesius* and *P. laetus* to be parallel developments from a form similar to *P. kingii* while the contingency of a close relationship between *P. caesius* and *P. bridgesii* would be more remote. A more probable connection exists between *P. caesius* and *P. gracilentus,* which view gains support from consideration of the scape-like inflorescence, scarcely ampliate corolla well ridged within, and the bearded orifice common to these species, and their proximal geographic distribution. The species is remarkably uniform with no noteworthy variants.

4. **Penstemon scapoides** sp. nov.

Herba perennis, 2.5–4.5 dm. alta; rhizomatibus prostratis moderati lignescentibus, ramosis, nigrescentibus, facile diffractis; caulibus erectibus, usque ad basim inflorescentiarum glaberrimis, gracilibus, simplicibus, viridibus; foliis oppositis, integris, basilibus ovatis vel subrotundatis, apice retusis, 5–15 mm. longis, omnino canescentibus, petiolis gracilibus, laminis aequalibus vel paulo longioribus, caulinis sessilibus, oblanceolatis, lineari-lanceolatis, paucibus (1–3 geminis), prope inflorescentiam gradatim reductis, glabratis; inflorescentiis glandulari-pubescentibus, laxe paucifloris, ramis laxe ascendentibus; calycibus 3–5 mm. longis; corollis 27–35 mm. longis, violaceo-coeruleis, exteriore paulo glandulari-pubescentibus; faucibus ventrali plicatibus flavo-pubescentibusque; staminibus sterilibus (in floribus quibusque singulis) apice dense flavo-barbatis; antheris ab apice ad *ca.* dimidiam superam marginaliter dehiscentibus; capsulis ignotis.

Type: Westgard Pass, 11.5 miles northeast of Big Pine, Inyo County, California, at 2130 m. (7000 ft.) altitude, June 22, 1930, *David D. Keck* 545 (Dudley Herbarium of Stanford University, No. 185574; isotypes Berlin, CA, CI, G, Kew, Miss, NY, Phila, Po, UC). Growing in a rock-bound desert canyon of the Upper Sonoran Zone on gravelly slopes with *Pinus monophylla, Artemisia tridentata, Ephedra viridis,* and *Penstemon bridgesii.* Common in a patch about 50 meters square but not observed elsewhere in this canyon.

Collected also about ten miles due north of the type locality on Wyman Creek, White Mountains, at 2900 m. (9500 ft.) alt., *Duran* 1737 (private herbarium of Victor Duran, University of California). Mr. Duran, who has made intensive field studies in the White Mountains for several seasons, notes, "Common in this canyon only, as far as I have seen." Other collections studied are: type locality, *Duran;* same locality, June 4, 1924, *Jones* (Po); Lida, Esmeralda County, Nevada, June 4, 1924, *Jones* (Po).

This species is marked by the dense tufts of grayish, soft-canescent leaves that cover the numerous, very short, sterile shoots arising from the horizontal rootstocks. These leaves, with their rotund blades and

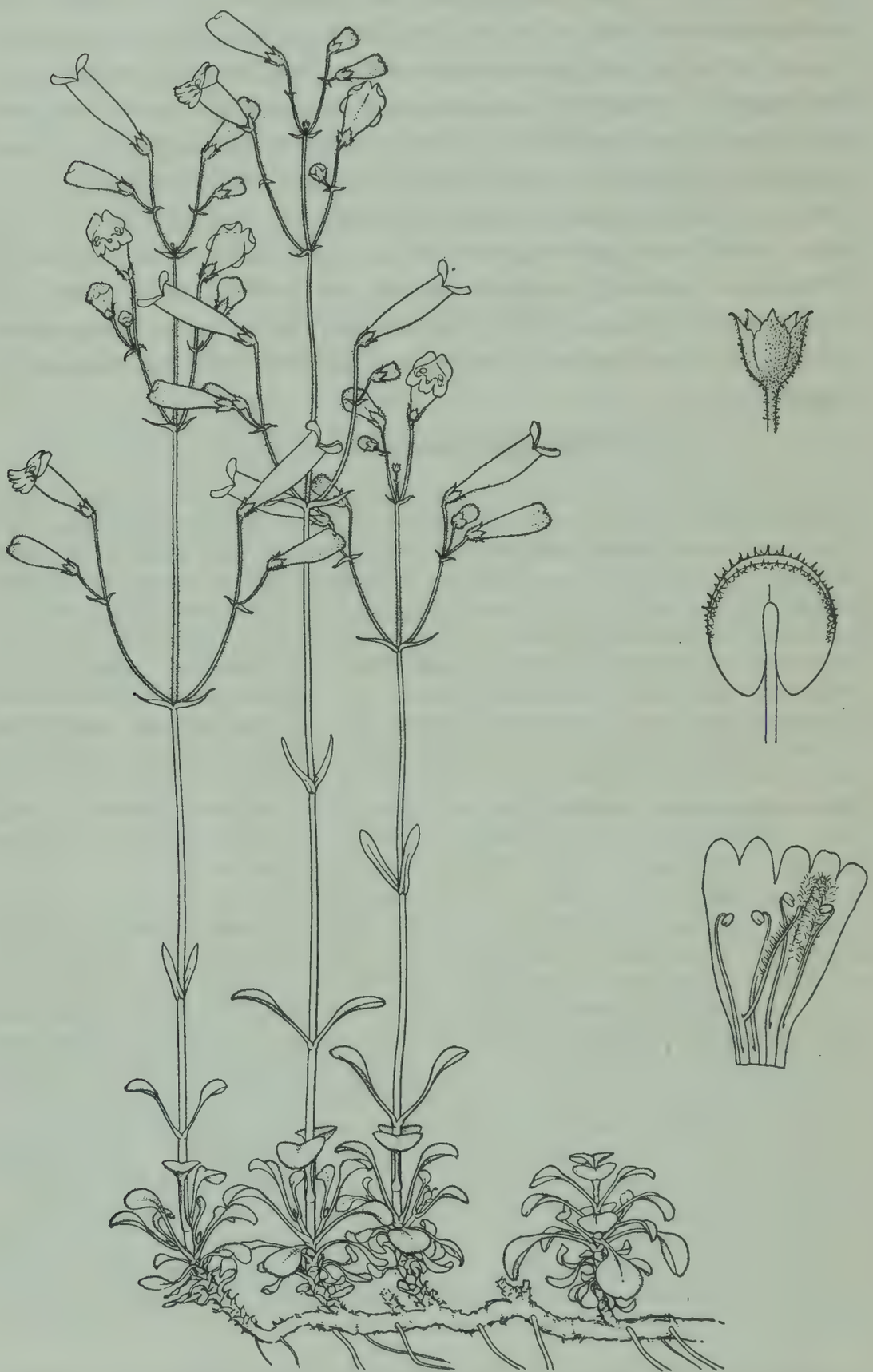


Fig. 4. *P. scapoides* Keck from the type collection. Habit × *ca.* ½; corolla opened longitudinally × *ca.* 1; calyx × *ca.* 2; anther × *ca.* 10.

long petioles, are similar to those of *P. purpusii,* and, except for their pubescence, to those of *P. caesius.* The scape-like flowering stems are quite glabrous from the base to the first branches of the inflorescence, but are often sparsely glandular immediately above the nodes. There are usually but two pairs of leaves above the basal tuft on the flowering stems. The sepals, which resemble those of *P. caesius,* are oblong or ovate with obtuse or acute tips, and are entirely herbaceous or obscurely hyaline only along the entire or moderately erose margins. The corolla of this species is not deeply colored, the pale lilac limb and throat contrasting with the short, red-lilac tube which is yellow within the protection of the calyx. Ventrally, the throat is nearly white, and additionally characterized by two prominent, longitudinal ridges moderately bearded for almost their full length.

The nearest known relative of this species is *P. caesius,* in fact, these are more closely related to each other than to any third species. If the assumption is correct, that *P. caesius* is derived from such a type as *P. gracilentus,* then *P. scapoides* is doubtless a derivative of *P. caesius.* At all events it is further separated from *P. gracilentus* in all characters than is *P. caesius.* The only alternative is the suggestion that *P. scapoides* was derived from *P. kingii,* and *P. caesius* from *P. scapoides.* But the great morphologic gap existing between the first two named is sufficient to make such a proposal untenable in the light of present knowledge.

5. **Penstemon cusickii** Gray

Penstemon cusickii Gray, Proc. Am. Acad. 16:106, 1880.

Penstemon macbridei A. Nels., Bot. Gaz. 52:272, 1911. The type, from Big Willow, Idaho, cannot be separated by morphologic characters from the type of *P. cusickii,* or can the other Idaho collections studied.



Fig. 5. *P. cusickii* Gray. Anther × 10.

Perennial herb or subshrub 2–4 dm. high: herbage gray-green, not glaucous, hirtellous throughout: herbaceous shoots unbranched to inflorescence: leaves 3–6.5 cm. long, 2–8 mm. wide, linear to narrowly

oblanceolate, or some of lower spatulate: calyx glabrous or minutely puberulent, 3.5–7 mm. long; sepals broadly lanceolate to orbicular, acuminate or merely acute: corolla bright blue with purple tube, 15–20 (–23) mm. long, 7–10 mm. wide at summit of throat: lower pair of stamens exceeding throat, upper pair equaling it or nearly so; anthers retuse at apex, sparingly short-hirsute at sinus.

Locally common on hillside slopes, usually in the sagebrush climax, in southwestern Idaho and adjacent eastern Oregon, at elevations of 600–1400 m. "On the banks of Powder River or Eagle Creek, N. E. Oregon, June, 1880, Cusick."

IDAHO. Blaine County: near Camas Prairie on Camp Creek, *Macbride & Payson* 2949 (CA, DS, G, Po, RM, UC). Elmore County: Regena, *Macbride & Payson* 2841 (G, RM). Gem County (?): Boise-Payette Project (Sand Hollow), *Macbride* 876 (DS, G, Po, RM, UC). Washington County: Mann's Creek, July 8, 1899, *Jones* (Po). Canyon County: Big Willow, *Macbride* 105 (RM, type of *P. macbridei;* isotypes at DS, G, UC). OREGON. Baker County: slopes of Powder River or Eagle Creek, June, 1880, *Cusick* (G, type); between Baker and Pleasant Valley, *Applegate* 6261 (DS); Burnt River and southward, *Cusick* 1621 (DS, UC); Huntington, *Holway* 71 (UO). Malheur County: near Ironside, *Henderson* 9137 (CA); Jordan Valley Highway, near Malloys, *Henderson* 9148 (CA, UO).

The importance of this species is that it represents the probable ancestral type from which the majority of species in the section *Saccanthera* have arisen. The restricted distribution, now confined to the sagebrush country about the Snake River and its upper tributaries, and the lack of variation suggest that this is a relict. *Penstemon kingii* of Nevada, and *P. leonardii,* of the Utah region, are its closest relatives. The former is similar in habit, shape of leaves, shape and color of corolla, and a few minor similarities; but is readily distinguished from *P. cusickii* by the glandular-pubescent pedicel, calyx, and corolla. Also, it is usually distinguished by its holosericeous herbage, narrow sepals, and very small anthers; but these are not always differentials, for *P. cusickii* displays considerable variability in these same features. A marked similarity exists between these two, however, and as the range of *P. kingii* is two hundred miles south of *P. cusickii,* with no important barriers between, and the two choose similar habitats, the probability of their rather recent segregation is apparent. *Penstemon leonardii* is not as closely related to *P. cusickii* for it is a glabrous-leaved species of the mountains, but it would seem to be a direct derivative, nevertheless.

The nearest relative of *P. cusickii* outside of this section appears to be in the section *Graciles* with such a species as *P. radicosus* of the *P. humilis* group. In most features these are very comparable. *Pen-*

stemon cusickii and the members of its derived line have lost the beard found on the sterile filament in the section *Graciles* except for an occasional reversion found even in the most specialized species of the series.

The evolution of the anther also indicates that *P. cusickii* is primitive. In the section *Graciles,* the anther is dehiscent to the base, more or less explanate, and not margined with subulate processes. In *P. cusickii* and its nearest relatives, the anther is dehiscent merely across the apex but is as widely gaping as possible and there are minute subulate processes along the line of dehiscence. In the more specialized species of the line evolved from *P. cusickii,* the anther is larger, more complex, dehiscent further toward the base but not gaping as widely in proportion, and the subulate processes along the line of dehiscence are prominent.

If, as has been mentioned, *P. gracilentus* has been derived from such a species as *P. procerus,* and *P. cusickii* from *P. radicosus,* the lines in the subsection *Heterophylli* had slightly different starting points, as judged from the present evidence. As retraced, the three lines of *Heterophylli* (including the line of *P. diffusus*) converge almost immediately after their entrance into the section *Graciles,* so a genetic explanation for their unusual development is not difficult to find.

6. **Penstemon leonardii** Rydb.

Penstemon leonardii Rydb., Bull. Torr. Club 40:483, 1913.



Fig. 6. *P. leonardii* Rydb. Anther × 13.

Perennial herb or subshrub 1.5–4 dm. high: herbage bright or dark green, not glaucous, glabrate to somewhat hispidulous on younger shoots particularly toward their bases, but leaves glabrous except for scaberulous margins and granules on upper side along midrib: herbaceous shoots unbranched to inflorescence: leaves 1.5–6 cm. long, 4–10 mm. wide; lower oblanceolate to spatulate; upper oblanceolate to narrowly elliptic, tapering more to base than to apex: calyx glabrous except for granular glands at very base, 3.5–6 mm. long; sepals lanceolate, with slightly scarious margins and attenuate tip: corolla deep blue with throat violet-blue and tube violet, 15–18 mm. long, 6–8 mm. wide at

summit of throat: lower pair of stamens exceeding throat, half again as long as upper pair enclosed in throat; anthers retuse at apex, sometimes rounded, sparingly short-hirsute or usually glabrous at sinus, 1.1–1.35 mm. long, the teeth irregularly distributed along the widely gaping line of dehiscence.

Frequent in rocks or gravelly situations on both slopes of the Wasatch Mountains from southeastern Idaho to southern Utah County, Utah, reappearing in Kane and Washington counties, southwestern Utah, at elevations of 2000–3000 m. "Utah: Diehl's Grove, Wahsatch Mountains, Aug. 1, 1884, *Leonard* (type, in herb. N. Y. Bot. Gard.)"

UTAH. Morgan County: Peterson Canyon, *Pammel & Blackwood* 3866 (G). Salt Lake County: Parley's Canyon, *Pennell* 5961 (DS), 5953 (G, RM); Parley's Park, *Watson* 788 (G, distributed as a cotype of *P. kingii* Wats.); Altus, July 7, 1908, *Clemens* (DS). Wasatch County: Snake Creek Canyon, above Midway, *Keck* 719 (CI, DS, CA, G, Kew, Berlin, Miss, Phila, Po, UC). Utah County: Aspinwall Peak, American Fork Canyon, July 15, 1895, *Jones* (Po, DS); above Aspen Grove, northeast of Mount Timpanogas, *Keck* 733 (CI, DS, Phila, Po, UC); Strawberry Summit, *Keck* 778 (CI, DS, Phila, CA, G, Miss, Po, UC). Kane County: 1873, *Meehan* (G). Washington County: Pine Valley Peak, *Purpus* 6193 (UC).

It has been pointed out under *P. cusickii* that *P. leonardii* is to be considered a derivative of that species. These species are similar in habit, leaf-shape, corolla-color, and anther-shape, to mention the most important characters, while differences occur in pubescence characters, shape of sepals, and relative length of the stamen pairs, as well as in geographic distribution and habitat. *Penstemon platyphyllus* is very closely related to *P. leonardii*. A notable difference between these, one which field studies indicate as constant although herbarium material seldom discloses it, is in the color of the corolla. *Penstemon platyphyllus* has a lavender or light violet corolla with lobes of the same shade, whereas *P. leonardii* has a purplish blue with lobes distinctly blue, the purple becoming more pronounced through the throat toward the tube. The former species occurs at lower elevations and is marked by larger size in habit, leaves, corolla, and anthers, as well as by more slender, ascending stems, broader sepals, and additional anther characters.

7. **Penstemon platyphyllus** Rydb.

Penstemon heterophyllus var. *latifolius* Wats., Bot. King's Expl. 222, 1871.

Penstemon latifolius Krautter, Contr. Bot. Lab. Univ. Pennsylv. 3:194, 1908. (Not *P. latifolius* Hoffmg. 1824.)

Penstemon platyphyllus Rydb., Bull. Torr. Club 36:690, 1909. Based on *P. heterophyllus* var. *latifolius* Wats., the type is an isotype of that variety at New York Botanical Garden.

Perennial herb or subshrub 3–6 dm. high: herbage bright green, slightly glaucous, somewhat hispidulous on younger shoots particularly toward their bases, but leaves glabrous except for scaberulous margins and granules on upper side along midrib: herbaceous shoots unbranched to inflorescence: leaves 1.5–5.5 cm. long, 4–15 (–25) mm. wide; lower oblanceolate, spatulate, or obovate; upper lance-elliptic to elliptic-ovate, tapering equally to base and apex: calyx glabrous except for granular glands at very base, 3.5–5.5 mm. long; sepals lance-ovate to ovate, with moderately scarious margins and acuminate tips: corolla lavender or violet throughout, 22–25 (–30) mm. long, 8–11 mm. wide at summit of throat: lower pair of stamens exserted from throat, half again as long as upper pair enclosed in throat; anthers obtuse or rounded at apex, glabrous throughout or short-hirsute at and near sinus, 1.6–2.1 mm. long, the teeth regularly distributed along the scarcely gaping line of dehiscence.

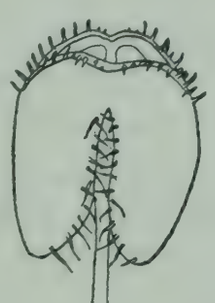


Fig. 7. *P. platyphyllus* Rydb. Anther × 10.

Common in rocky soil on the western slope of the Wasatch Mountains from Weber to Utah counties, and in the Ibapah Range of western Tooele County, Utah, and eastern Nevada, at elevations of 1500–2400 m. "Wahsatch Mountains, 5–8,000 feet altitude; July, August. (787.)" (*Watson* 787, type.)

UTAH. Davis County: Farmington Canyon, *Pammel & Blackwood* 3659 (CA). Salt Lake County: Parley's Canyon, *Pennell* 5957 (DS, G, RM); Cottonwood Canyon, *Watson* 787 (G, isotype, type of *P. heterophyllus* var. *latifolius* Wats.); Big Cottonwood Canyon, *Pennell* 6067 (G, RM), *Keck* 748 (CI, DS, CA, G, Kew, Berlin, Miss, Phila, Po, UC); Little Cottonwood Canyon, *Keck* 741 (CI, DS, Phila, Po, UC, CA, G, Miss). Utah County: American Fork Canyon, *Jones* 1888 (CI, DS, Po), *Keck* 740 (DS, CI, Phila, Po, UC). Tooele County: Mount Ibapah, July 17, 1903, *Jones* (Po). NEVADA. White Pine County (?): Spring Creek, June 23, 1891, *Jones* (Po).

This species is considered a derivative of *P. leonardii* as has been pointed out under the latter.

8. **Penstemon sepalulus** A. Nels.

Penstemon azureus var. *ambiguus* Gray, Syn. Fl. 2[1]:272, 1878.

Penstemon sepalulus A. Nels., New Man. Rocky Mount. 449, 1909. Based primarily upon *P. azureus* var. *ambiguus* Gray.

Subshrub 4–8 dm. high: herbage grayish, blue-glaucous, glabrous throughout: new shoots corymbosely branching from near the base to the inflorescence with the twigs ascending, less commonly unbranched: leaves of one kind, 3–8 cm. long, 3–10 (–13) mm. wide, linear to narrowly elliptic, acute at each end: calyx glabrous, 1.8–3.2 mm. long; sepals obovate or widely oblong, truncate at tip except for small mucronation: corolla pale lavender to pale violet with tube deep lavender, red-lavender, or red-violet, 20–25 (–28) mm. long, 8–12 mm. wide at summit of throat: lower pair of stamens exserted from throat, half again as long as upper pair enclosed in throat; anthers rounded at apex, glabrous throughout.



Fig. 8. *P. sepalulus* A. Nels. Anther × 10.

Frequent in rocky or gravelly locations, being particularly found on steep rock slides through which these plants send tremendous, woody root-systems, on the western slopes of the Wasatch Mountains, and on Mount Nebo, from Salt Lake to Juab counties, Utah, at elevations of 1200–2250 m. No type given but the general range as follows: "In the mountains of northwestern Colorado, in adjacent Utah and Wyoming." Based primarily upon *P. azureus* var. *ambiguus* Gray, of which the type locality is: "Cañons of the Wasatch Mountains, Utah, viz of the Provo and American Fork, *Watson.*"

UTAH. Utah County: American Fork Canyon, *Jones* 1883 (CA, DS, Po), *Keck* 739 (CA, CI, DS, G, Kew, Miss, Phila, Po, UC); Provo Canyon, *Watson* 786 (G, type of *P. azureus* var. *ambiguus* Gray), *Pennell* 6110 (DS, G, RM); six miles from Spanish Fork toward Thistle, *Keck* 712 (CA, CI, DS, G, Berlin, Kew, Miss, Phila, Po, UC). Juab County: Mount Nebo, July 19, 1910, *Jones* (Po).

It sems likely that *P. sepalulus* is the last species in the line from *P. cusickii* through *P. leonardii* and *P. platyphyllus.* The greatest morphologic gap in this line is between *P. cusickii* and *P. leonardii* which might be considered as proportionate to the geographic differences between them. *Penstemon platyphyllus* is a species of lower altitudes than *P. leonardii* and is quite intermediate in habit and

stature between that species and the tall and slender *P. sepalulus*. *Penstemon platyphyllus* differs from the blue-flowered *P. leonardii* in bearing light-violet corollas and this new shade has become even lighter, if anything, in *P. sepalulus*. The latter species is distinguished by the very small sepals and the glaucous character as well as by the tall habit and slender, wand-like branches.

It is not surprising to find natural hybrids occurring between closely related and adjacent species. Two collections have been studied that appear to be such between *P. platyphyllus* and *P. sepalulus*, one from the Deep Creek Mountains, southwestern Tooele County, Utah (Oct. 11, 1901, *Jones*, Po), the other from Cottonwood Canyon, Salt Lake County (Sept. 7, 1896, *Stokes*, DS). In these, the characters of the two species seem to be about equally distributed in the hybrids. Typical *P. sepalulus* has not been seen from the region of the Deep Creek range.

9. **Penstemon kingii** Wats.

Penstemon kingii Wats., Bot. King's Expl. 222, 1871. The original description of this species was evidently drawn from two distinct plants, the "pruinose- or glandular-pubescent" one from Nevada, and *P. leonardii* from Utah. Since the Utah species does not fit this description of pubescence, *P. kingii* is here considered the proper designation for the Nevadan material.

Penstemon roezlii var. *violaceus* Brandegee, Bot. Gaz. 27:456, 1899. This matches the material from eastern Nevada and can not be separated from it. The type came from "Oriental, Gold Mountain, Nevada, *Dr. C. A. Purpus*, no. 5995."

Penstemon violaceus A. Nels., Proc. Biol. Soc. Wash. 17:96, 1904. Based upon *P. roezlii* var. *violaceus* Brandegee.

Perennial herb 0.7–2.5 (–4) dm. high, lignescent at base, with few to several erect or ascending stems from the central crown: herbage gray-green, hoary with spreading hairs, glands only in the inflorescence: woody portion mostly subterranean, the stems 3–8 mm. in diameter, with thin grayish brown bark; flowering shoots herbaceous, usually slender, usually noticeably purplish: leaves of one kind, evenly distributed along stem, soft, entire, linear-lanceolate to oblanceolate, 20–40 (–65) mm. long, 4–7 (–14) mm. wide, narrowed to a petiole-like base, acute or obtuse at apex, merging into the smaller bracts of inflorescence: inflorescence a panicle 3–10 (–22) cm. long, hirtellous throughout, with stipitate clavate glands only on the outside of corolla, calyx, and summit of pedicel; peduncles bearing 1 or 2 (rarely more) flowers, and usually less than 1 cm. long, rather divergent from the main axis; pedicels very short: calyx purple or green, 4–6 (–8) mm. long; sepals lanceolate to narrowly ovate, attenuate or acute, herbaceous, the margins rarely narrowly hyaline, entire: corolla dark violet becoming whitish at base of tube, with buds the same shade, 14–20 mm.

long, 5–8 mm. wide at summit of throat, slightly glandular-pubescent without, glabrous within, moderately ampliate; throat twice as long as tube; lips equal, 4–7 mm. long, the lobes spreading moderately, all cleft less than half the length of lips: lower pair of stamens equaling throat, upper pair nearly as long; filaments glabrous, the sterile one slightly dilated at the glabrous tip, extending as far or farther anteriorly than the fertile ones; anthers making a ¾ circle in outline, retuse at apex, 1.1–1.2 mm. long, glabrous, dehiscent merely across apex of sacs, scarcely gaping, the teeth on line of dehiscence inconspicuous, the longest 0.1 (rarely 0.15) mm. long; capsule ovate, 6–10 (–12) mm. long: seeds 25–50 per capsule, irregular, 1.2–2.2 mm. long, the seed-coat gray or buff.



Fig. 9. *P. kingii* Wats. Anther × 13.

Rare and local in the sagebrush-juniper belt on various ranges from southern Elko County to southern Esmeralda County, Nevada, at elevations of 1500–2000 m. "From the West Humboldt Mountains to Monitor Valley, Nevada, and in the Wahsatch and Uintas" (the latter referring to *P. leonardii* Rydb.); "6–7,000 feet altitude; June, July. (788.)" (*Watson* 788.)

NEVADA. Elko County: Harrison Pass Ranger Station, Ruby Mountains, June 16, 1928, *Borrell* (CI). Eureka County: Emigrant Pass, Tuscarora Mountains, *Mason* 4628 (CI), *Keck* 936 (CI, DS, Phila, G); Palisade, June 14, 1882, *Jones* (Po). Lander County: Battle Mountain, June 15, 1882, *Jones* (Po). Humboldt County: Coyote Mountains, *Watson* 788 (New York Botanical Garden, isotype). Esmeralda County: Gold Mountain, near Oriental, *Purpus* 5995 (UC, type of *P. roezlii* var. *violaceus;* isotype Po).

The line of dehiscence and other characters of the anther place *P. kingii* with the other Great Basin species. Its connections with *P. cusickii* have been pointed out under the latter, and its connections with the California species will be considered under *P. laetus.*

This species is relatively litle known as yet, but it seems very likely that it is much more wide-spread over central Nevada than the few collections made would indicate. Many mountain ranges in that state have been quite inaccessible to collectors, but as botanical exploration continues we may expect additional records of the occurrence of this interesting species.

10. **Penstemon laetus** Gray

Figures 10 to 12

Penstemon laetus Gray, Proc. Boston Soc. Nat. Hist. 7:147, 1859.

Suffrutescent subshrub 2–8 dm. high: herbage gray- or yellow-green, the older parts becoming purplish, not glaucous, finely pubescent with short white hairs, rarely glabrate, always glandular-pubescent in inflorescence: leaves all of one kind, linear to oblong or oblanceolate (filiform in subsp. *filiformis*), or the lower oblanceolate, the upper lanceolate, 1.5–6 (–12) cm. long, 1.5–10 (–15) mm. wide; upper cauline leaves sessile or somewhat clasping, often noticeably widest, or flaring, at base: peduncles divergent from main axis: calyx 4–8 mm. long; sepals linear-lanceolate to narrowly ovate or oblong, acute or attenuate, the margins entire and rarely narrowly hyaline: corolla bluish lavender to bluish violet, with purplish tube, and dark blue lobes, slightly glandular-pubescent without: lower pair of stamens equaling throat, upper pair ⅔–⅘ as long; anthers broadly ovate (sagittate in subsp. *sagittatus*) dehiscent ½–⅘ the length of sacs, the teeth on line of dehiscence mostly in one rank and inconspicuous.

From central Oregon south through the Sierra Nevada to the Tehachapi Mountains of southern California; west from Siskiyou County to Humboldt County, California; east from the mountains into Nevada in the vicinity of Lake Tahoe.

Key to the Subspecies of Penstemon laetus

A. Anthers broadly oval or ovate in outline, about as broad as long, dehiscent ½–⅗ their length; corolla-throat not constricted at junction with lip, the lips gaping.

B. Leaves linear or wider, 2–12 mm. wide, often folded along midrib but margins not involute; corolla 14–30 mm. long.

C. Corolla 14–20 mm. long ..... 10*a*. **roezlii**

CC. Corolla 20–30 mm. long.

D. Calyx 4–8 mm. long; sepals lanceolate or broader, acute or acuminate. 10*b*. **typicus**

DD. Calyx 8–15 mm. long; sepals linear-lanceolate, attenuate. 10*c*. **leptosepalus**

BB. Leaves all filiform, 0.5–2 mm. wide, margins usually involute; corolla 14–20 mm. long ..... 10*d*. **filiformis**

AA. Anthers narrowly sagittate, ½–⅔ as broad as long, dehiscent ⅗–⅘ their length; corolla 20–30 mm. long; throat somewhat constricted at junction with lip, the lips scarcely spreading ..... 10*e*. **sagittatus**

10a. **Penstemon laetus** subsp. **roezlii** (Regel) comb. nov.

Penstemon roezlii Regel, Gartenflora 21:239, 1872.

Penstemon heterophyllus var. (?) Torr. et Gray, Pacif. Rail. Rep. 2:122, 1855. This is referred to *roezlii* by Gray in the Synoptical Flora, and I have seen the type in Herb. Gray.

Penstemon cinerascens Greene, Leaflets 1:161, 1906. Type (*Baker* 1144) from Spooner, Douglas County, Nevada. Four isotypes examined. This is the grayer form of *roezlii*, its heavier puberulence, and leaves half-folding along the midrib, probably being adaptations to an arid environment.

Penstemon laetus of Krautter, Contr. Bot. Lab. Univ. Pennsylv. 3:190, 1908, as regards Nevada material.

Penstemon laetus var. *roezlii* Jepson, Man. Calif. 916, 1925.

Penstemon gracilentus var. *ursorum* Jepson, l. c. Type locality, Bear Valley, Nevada County, California, 4500 ft., *Jepson*. Type studied. This, together with all *laetus* material, differs from *gracilentus* in having a glabrous sterile filament. The type is very typical of *roezlii* excepting that the leaves are somewhat glaucous, a common feature in this subspecies.

Penstemon laetus of Jepson, l. c., as regards material north of Plumas County and east of the Sierran divide, California.

Lower leaves linear to oblanceolate, and upper lanceolate, margins not involute, 2–7 cm. long, 2–12 mm. wide: inflorescence usually a mixed panicle, broadest at base, often reduced to a simple panicle or even a raceme; peduncles bearing 1–4 flowers, the pedicels usually elongated so flowers well separated on peduncle: calyx 4–7 mm. long; sepals lanceolate to oblong, acute or acuminate: corolla 14–20 mm. long, 5–9 mm. wide at throat when pressed, gaping: anthers broadly ovate, dehiscent ½–⅗ their length.



Fig. 10. *P. laetus* subsp. *roezlii* Keck. Anther × 10.

Common from the low mountains of south-central Oregon to the Sierra Nevada of the Lake Tahoe district of California, at elevations of 600–2500 m.; in northern California on both slopes of the Sierra, but toward its southern limits more restricted to the eastern side of the mountains, extending the range slightly into Nevada. "Die Samen sammelte Roezl in der Sierra-Nevada, Californiens."

OREGON. Wheeler County: 7 miles E. of Mitchell, *Peck* 10115 (DS). Lake County: Button Springs, *Leiberg* 408 (Po, G, DS).

Klamath County: Keno, *Cusick* 2836 (UC, G, Po). Jackson County: Emigrant Creek, near Ashland, *Applegate* 2218 (DS). Josephine County: Kerby, *Kildale* 8166 (DS). CALIFORNIA. Sierra Nevada, *Roezl* (G, fragment and drawing of type). Modoc County: Mount Bidwell, *Manning* 176 (UC). Siskiyou County: Goosenest Mountains, *Butler* 1579 (DS, G, Po, RM, UC). Trinity County: Dorleska, Salmon Mountains, *Hall* 8568 (UC). Lassen County: 12 miles west of Susanville, *Keck* 954 (CA, CI, Berlin, DS, G, Miss, Kew, Phila, Po. UC). Plumas County: Sloat, *Keck* 444 (Berlin, CI, DS, G). Yuba County: Challenge, *Keck* 982 (CI, DS, Miss, Phila, Po, UC). Nevada County: Bear Valley, July 1898, *Jepson* (Jepson Herb., type of *P. gracilentus* var. *ursorum* Jepson). Placer County: Donner Lake, *Heller* 6925 (DS, G, Po, RM, UC). Amador County: Silver Lake, *Mulliken* 120 (UC). Alpine County: above Hermit Valley, *Hall & Chandler* 4771 (UC). Inyo County: Andrews Camp, upper Bishop Creek, July 1913, *Brandegee* (UC). NEVADA. Washoe County: Verdi, *Heller* 10879 (DS, G, UC). Douglas County: Spooner, *Baker* 1144 (G, Po, RM, UC, isotypes of *P. cinerascens* Greene).

It appears that this subspecies is more variable in Oregon than in California. The Sierra Nevada material is quite uniform, but that of the Klamath Mountains is apt to display slight differences at each appearance in a different chain or spur. These variations are in the shape and size of the anther or of the corolla, or in a reduction of the compound inflorescence to a subracemose type, etc. Variants of this sort are considered to be genetically fixed, as strong tendencies for certain variations to be geographically segregated are noted, and also, the stability of these characters has been observed in California material of *roezlii,* when it has been grown under various ecologic conditions in experimental gardens. But these variations are not sufficiently marked to warrant nomenclatorial recognition. The material from central Lake County, Oregon, is noteworthy, for here the flowers may be as large as those in *sagittatus,* but with the throat more inflated as in *typicus,* and the anthers are larger than the characteristic ones of *roezlii.* The intermediate forms in Klamath County probably outnumber the extremes in Lake County, so the segregation is not sufficiently distinct for nomenclatorial consideration. This deviation from *roezlii* may be considered morphologically parallel to that resulting in subsp. *sagittatus,* but it has not progressed nearly as far.

10b. **Penstemon laetus** subsp. **typicus** nom. nov.

Penstemon laetus Gray, l. c.

Penstemon dimorphus O. Kuntze, Rev. 2:463, 1891. "U. St.: Yosemite Thal 1000 m." No type is mentioned.

Penstemon roezlii of Krautter, Contr. Bot. Lab. Univ. Pennsylv. 3:191, 1908, as regards Kern County material.

Lower leaves linear to oblanceolate, and upper lanceolate, margins not involute, 2–10 cm. long, 2–12 mm. wide: inflorescence usually a narrow panicle or reduced almost to a raceme; peduncles mostly 1-flowered, the pedicels usually very short, so flowers usually subsessile on peduncles: calyx 4–8 mm. long; sepals lanceolate to oblong, acute or acuminate: corolla 20–30 mm. long, 8–12 mm. wide at throat when pressed, gaping: anthers broadly acute, dehiscent ½–⅗ their length.



Fig. 11. *P. laetus* subsp. *typicus* Keck. Anther × 10

Plentiful at elevations of 600–2500 m., on the western slope of the Sierra Nevada from eastern Yuba County to the Tehachapi Mountains and Frazier Mountain, Ventura County, California. "L. J. Xantus at Fort Tejon and vicinity, California."

CALIFORNIA. Yuba County: Timbuctu, *Applegate* 5377 (DS). Eldorado County: Sly Park, *Hall* 11374 (CA, UC). Calaveras County: near Murphy, *Stanford* 396 (DS, Po). Tuolumne County: Pate Valley, *Keck* 275 (CI, DS, G, Kew). Mariposa County: Yosemite Valley, *Abrams* 4404 (DS, G, Po, UC). Madera County: Longworthys, near Northfork, *Abrams* 4947 (DS, G). Tulare County: Giant Forest, *Dudley* 2976 (DS). Kern County: Fort Tejon, *Xantus* (G, type), *Hall* 6268 (DS, UC, RM). Ventura County: Frazier Mountain, *Hall* 6609 (DS, UC).

Within the southern half of its range this subspecies is characterized by larger corollas and leaves than the material from further north. The increase in size is gradual as one proceeds from north to south, with apparently no abrupt variations. In fact the differences might well be entirelly overlooked unless one compared collections from Mariposa County northward with those from Kern County. There is an increase in size of material from east to west parallel to

that from north to south if the occurrence of the subspecies is studied in a transect down the western slope of the Sierran axis. For example, in Tuolumne County at about the 2600 m. (8500 ft.) level this subspecies is represented by a dwarfed form that is smaller in all its notable features, including the corolla and its parts, than the subspecies as it occurs directly to the west at the 1500 m. (5000 ft.) level. The dwarfed form meets all the key's requirements for subsp. *roezlii*, but its relationship or origin is evidently with *typicus*, for there is a geographically and morphologically continuous series between it and *typicus* whereas there is a significantly wide geographic break between it and *roezlii*.

10c. **Penstemon laetus** subsp. **leptosepalus** (Gray) comb. nov.

Penstemon laetus var. *leptosepalus* Gray, Syn. Fl. 2[1]:442, 1886. The name was taken from Greene, in herbarium.

Lower leaves oblanceolate and upper lanceolate, margins not involute, 3–12 cm. long, 4–15 mm. wide: inflorescence an elongated simple or mixed panicle; peduncles bearing 1–4 or more flowers; the pedicels 1–10 mm. long, so flowers separated on peduncle: calyx 8–15 mm. long; sepals linear-lanceolate, attenuate: corolla 20–32 mm. long, 8–12 mm. wide at throat when pressed, gaping: anthers broadly ovate, dehiscent ½–⅗ their length.

From southern Tehama and western Plumas counties, through eastern Butte County, into Nevada and Placer counties, California, at elevations of 750–1700 m. "Butte County, California, *Mrs. Austin.*"

CALIFORNIA. Tehama County: Red Bluff, June 1917, *Wickes* (CA). Plumas County: Soapstone Ridge, *Heller* 12073 (CA, DS, G). Butte County: 1883, *Austin* (G, type of two sheets; isotype UC); Chaparral, *Keck* 972 (Berlin, CA, CI, DS, G, Kew, Miss, Phila, Po, UC); Forbestown, *Keck* 981 (CI, DS, Miss, Phila, Po, UC). Yuba County: Bullards Bar Reservoir, *Keck* 983 (CI, CA, DS, G, Miss, Po, Phila, UC). Placer County: between Colfax and Forest Hill, *Smith* 1879 (CA).

This subspecies is amply separated morphologically in the center of its distribution where it is geographically isolated from its relatives. But there are large areas where it grows with, or near, *typicus* and *roezlii*, and in addition *P. neotericus*. Apparently hybrid combinations are of frequent occurrence here with subsequent obscuring of the taxonomic criteria. The relative length of the sepal may be considerably modified but the characteristic linear-lanceolate outline of the organ appears to be more stable for it appears on very short sepals from these areas where the subspecies overlap. The criteria pointed

out for this subspecies in the key and description are considered of sufficient merit to warrant the subspecific rank because of their pronounced expression in this material which occurs to the north of the range of *typicus*. The attenuate sepals are not limited to *leptosepalus* in this species, for they occur, usually in less extreme form, in isolated collections through various portions of the range of *typicus*. The anthers of *leptosepalus* are like those of *typicus* (figure 11).

10d. **Penstemon laetus** subsp. **filiformis** subsp. nov.

Subsp. roezlii simillimus, sed foliis subfiliformibus, marginibus revolutibus, 2–7 cm. longis, ca. 2 mm. latis aut minoribus; calycibus 4–6 mm. longis, lobis lanceolatis, acuminatis aut acutis; corollis 13–17 mm. longis, faucibus 7–9 mm. diam.

Type: Between Lamoine and Sims in the belt of *Pinus ponderosa* and *Quercus garryana* in open stony places along the highway grade, Shasta County, California, June 24, 1916, *A. A. Heller* 12442 (Dudley Herbarium of Stanford University, No. 73526; isotypes CA, G).

The only other collection studied is from Shasta County, below Dunsmuir, *Hall* 4034*a* (UC). This fixes the range, as known at present, to the canyon of the Sacramento River for a distance not exceeding seventeen miles, in northern Shasta County.

This subspecies more closely resembles *roezlii* than it does the other subspecies of *laetus* and seems without doubt to have arisen from that. Its outstanding character is the filiform leaves, which are numerous, crowded on the stem, and mostly basal. They differ markedly from the usual type in *laetus,* and no intermediates have been found between this and the other subspecies. The inflorescence is a panicle or raceme, the peduncles usually bearing but one flower. The anthers of *filiformis* are of the *roezlii* type (see figure 10). It is noteworthy that subsp. *roezlii* is not known from the range of *filiformis,* so it would seem that the latter is geographically as well as morphologically separated from the former.

10e. **Penstemon laetus** subsp. **sagittatus** subsp. nov.

Penstemon laetus of Krautter, Contr. Bot. Lab. Univ. Pennsylv. 3:190, 1908, in part. Reference to *laetus* in Siskiyou County must include both subspecies *sagittatus* and *roezlii*, but the incomplete description does not differentiate between them. Krautter probably had *sagittatus* in mind as he treated *roezlii* separately, although hazily.

Corollis 20–30 mm. longis, 6–9 mm. latis; faucibus in latere superiore rectibus aut incurvatis, in latere inferiore ampliatus, sub limbo paululo constrictibus; labiis moderate ab quibusque divergentibus, non retroflexis; antheris sagittatis frequenter gracillimis, $\frac{3}{5}$–$\frac{4}{5}$ longitudinaliter dehiscentibus.



Fig 12. *P. laetus* subsp. *sagittatus* Keck. Anther × 10.

From southern Oregon into northern Shasta, Trinity, and Humboldt counties, California, at elevations of 450–1500 m.

Type: Mount Shasta, north side, Siskiyou County, California, altitude 5000–9000 ft. (1500–2700 m.), June 11, –16, 1897, *H. E. Brown* 360 (UC, No. 229876).

OREGON. Josephine County: Selma, *Kildale* 8915, 8860 (DS). CALIFORNIA. Siskiyou County: Shasta Valley, *Butler* 1338 (DS, Po, RM, UC); Cantara, *Eastwood* 1323 (CA, G); Preston Peak, *Kildale* 8668, 8717 (DS). Shasta County: below Dunsmuir, *Hall & Babcock* 4030 (UC). Del Norte County: Gasquet to Waldo, July 3, 1899, *Dudley* (DS); Gasquet Mountain, *Eastwood* 12128 (CA). Trinity County: Salmon Summit, junction of Siskiyou, Humboldt, and Trinity counties, *Kildale* 5361 (DS). Humboldt County: Klamath River, between Orleans and Somes Bar, *Chandler* 1472 (UC); Hupa Mountain, *Davy & Blasdale* 5666 (UC); between Three Creeks and mouth of Willow Creek, *Tracy* 3344 (UC); Grouse Creek, Aug. 1, 1888, *Chesnut & Drew* (UC).

The center of distribution of this subspecies is in the series of mountain chains of northwestern California known as the Klamath Mountains. Here the characters that mark this subspecies are very distinctive. The corolla, gradually curving upward and with an orifice of less diameter than the throat, has an appearance unlike that of the other subspecies; and the very narrow, deeply dehiscent,

acuminate-tipped anthers are also different. In habit the plant is often quite depressed, with ascending, slender branches. This habit is sometimes observed also in subsp. *roezlii.* The lower leaves are linear to oblanceolate and the upper lanceolate, which recalls its connection with *roezlii.* The peduncles, bearing from one to four flowers, suggest both *roezlii* and *leptosepalus,* while the occasional occurrence of attenuate sepals indicates a possible connection with *leptosepalus* although that character may well have arisen independently several times in this species. The flowers of *sagittatus* are considerably larger than those of *roezlii* but they are as large as only the smaller-flowered collections of *typicus,* such as those from Mariposa County northward. There is a wide geographic gap between *sagittatus* and the other large-flowered subspecies of *laetus,* but it occupies common territory with *roezlii,* particularly in the Shasta Valley and contiguous territory. Here the mixing of the two has doubtless caused the observed intermediate appearance of the anther. Neither the obtuse-angled shape characteristic of the *roezlii* anther, nor the acuminate-tipped shape of *sagittatus* appears to be dominant, for material that must be classed as *sagittatus* in its other characters has anthers better described as narrowly cordate than as sagittate.

Two minor variations of this subspecies deserve mention. One of these is from Salmon Summit via Horn Creek Trail, western Siskiyou County (*Kildale* 5361, DS). In this specimen the thick oblanceolate leaves are almost spatulate, obtuse, 2–3.5 cm. long, and 7–8 mm. wide. The anthers have many white hairs at the sinus, almost as long as the anther. In the typical subspecies, the leaves are thin and linear, or wider and tapering to base and apex, acute, 2–7 cm. long, and average 3 mm. wide. The anthers bear few to many dull or white hairs at sinus, usually much shorter than anther. The heavy twigs and leaves not in fascicles are not unique to this specimen as they are occasionally found in the typical form.

The second variation is from the bare easterly slope of Mount Eddy, Siskiyou County (*Heller* 13431, DS). It differs from the typical in appearing to be a dwarf type well suited to its habitat on fine gravel at 8000 feet (2450 m.) elevation. The old stems are decumbent and rooting and the many small oblanceolate leaves (not over 2 cm. long) extend up the stem only 6 or 7 cm. above the ground. The inflorescence is 4–5 cm. long with many large flowers about 25 mm. long.

Relationships of Penstemon laetus

Penstemon laetus subsp. *roezlii* extends into Nevada and from it the connections with the Great Basin species are traced rather clearly. The collections from upper Bishop Creek, Inyo County, California, and from Spooner, Douglas County, Nevada, are similar in having anthers almost as small as those of *P. kingii,* with very small teeth on the line of dehiscence. In the former specimen the anthers dehisce scarcely half their length, another character suggesting relationship with the more easterly species. *Penstemon kingii* is known to occur just over the Nevada line from Inyo County. Another striking similarity is that *P. kingii* is the one Great Basin species of this group in which glands in the inflorescence are most highly developed. This Spooner collection was selected by Greene for the basis of *P. cinerascens* (see synonymy of subsp. *roezlii*). The two collections, above mentioned, would certainly be referred to the same form. Their exceptionally small anthers are duplicated in material from as widely separated California stations as Lake Tahoe, northern Trinity County, and Modoc County. This results in the inevitable placement of *P. cinerascens* Greene in synonymy, as the vegetative peculiarities are of but little moment.

In most morphological characters, in addition to the similarities of anthers, *Penstemon laetus* subsp. *roezlii* resembles *P. kingii.* Doubtless one species has been derived from the other. The anther within *P. laetus* evolves from the type found in *P. kingii,* characteristic of that in the Great Basin and Utah species of the section, to a more broadly dehiscent form, usually with prominent teeth on the line of dehiscence and commonly with long white hairs at the junction of anther and filament. The anther types of the next four species have apparently had their inception within *P. laetus.*

Several closely related groups compose *Penstemon laetus.* The subspecies *roezlii* appears to be the most ancient form from which all the other subspecies have been derived with the possible exception of *leptosepalus.* Where *roezlii* occurs westward through the Sierra Nevada from the Lake Tahoe region, it meets the two subspecies *typicus* and *leptosepalus,* which replace it, for the most part, on the westerly slope of the mountains. From the point where the three meet, *typicus* extends southward and *leptosepalus* northward. Subspecies *typicus* is considered an expression brought out by the more

favorable western slopes of the Sierra Nevada in the form of larger flowers and greater vegetative growth. There has been a reduction in flower number along with their increase in size and consequent showiness. On the other hand, *leptosepalus* is a very robust form whose unusually long, attenuate sepals may be considered as derived from the oblong type. Probably this subspecies was derived from *typicus* rather than from *roezlii* although it combines some of the unique characters of each. It is probably younger than *typicus* for its range is quite restricted at present although it thrives under a variety of local conditions. In northern California and southern Oregon, *roezlii* has probably given rise to the subspecies *sagittatus*. The latter has most pronouncedly developed its peculiar anther and corolla characters in northwestern California. Subspecies *filiformis* appears to be a recent development from *roezlii*. The reduction in leaf-width is accompanied by an increase in the number of leaves.

11. **Penstemon neotericus**[5] sp. nov.

Frutex, 2–6 dm. altus, basim versus ramosus; caulibus multis erectis simplicibus, e basi usque ad inflorescentiam glaberrimis, coeruleo-glaucis; foliis integerrimis, basalibus anguste oblanceolatis aut spatulatis, petiolatis, 2–8 cm. longis, 3–9 mm. latis, caulinis anguste lanceolatis aut anguste ovatis, sessilibus; inflorescentiis glandulari-pubescentibus, ramis moderate divergentibus; calycibus 4–7 mm. longis; corollis 25–35 mm. longis, externe paulo glandulari-pubescentibus, interne glabris, lobis azureis, faucibus et tubo externe rubro-violaceis, interne albis; alabastris laete flavis; staminibus sterilibus (in floribus quibusque singulis) glaberrimis; antheris 2.5–3.25 mm. longis, ad sinus albo-hirsutis, ½–⅘ longitudinaliter dehiscentibus.

Extending from eastern Shasta County through northern Plumas County into Butte and Sierra counties, California, at elevations of 700–1850 m.

Type: Plumas County, halfway between Chester and Westwood, Lassen County, California, at 1465 m. (4800 feet) elevation, July 24, 1930, *David D. Keck* 958 (Dudley Herbarium of Stanford University, No. 185575; isotypes CA, CI, Berlin, G, Kew, Miss, NY, Phila, Po, UC).

CALIFORNIA. Lassen County: Martin Springs, Eagle Lake, *Brown & Weislander* 9 (Jepson); Westwood, *Feudge* 1768 (Po), *Keck* 957 (CA, CI, Berlin, DS, G, Kew, Miss, Phila, Po, UC). Shasta County: Montgomery Creek, June 13, 1923, *Bethel* (CA); E. slope Burney Mountain, *Applegate* 5856 (DS); Goose Valley, *Eastwood* 999 (CA, G); Lassen Peak, July 7, 1897, *Jones* (Po), *Austin* 646 (UC). Tehama County: Morgan Springs, *Eastwood* 1790 (CA). Plumas County: Lassen Peak, *Austin* 485 (UC); Chester, July 9, 1923, *Mack*

[5] The name *neotericus* is the Latin adjective meaning new, modern.

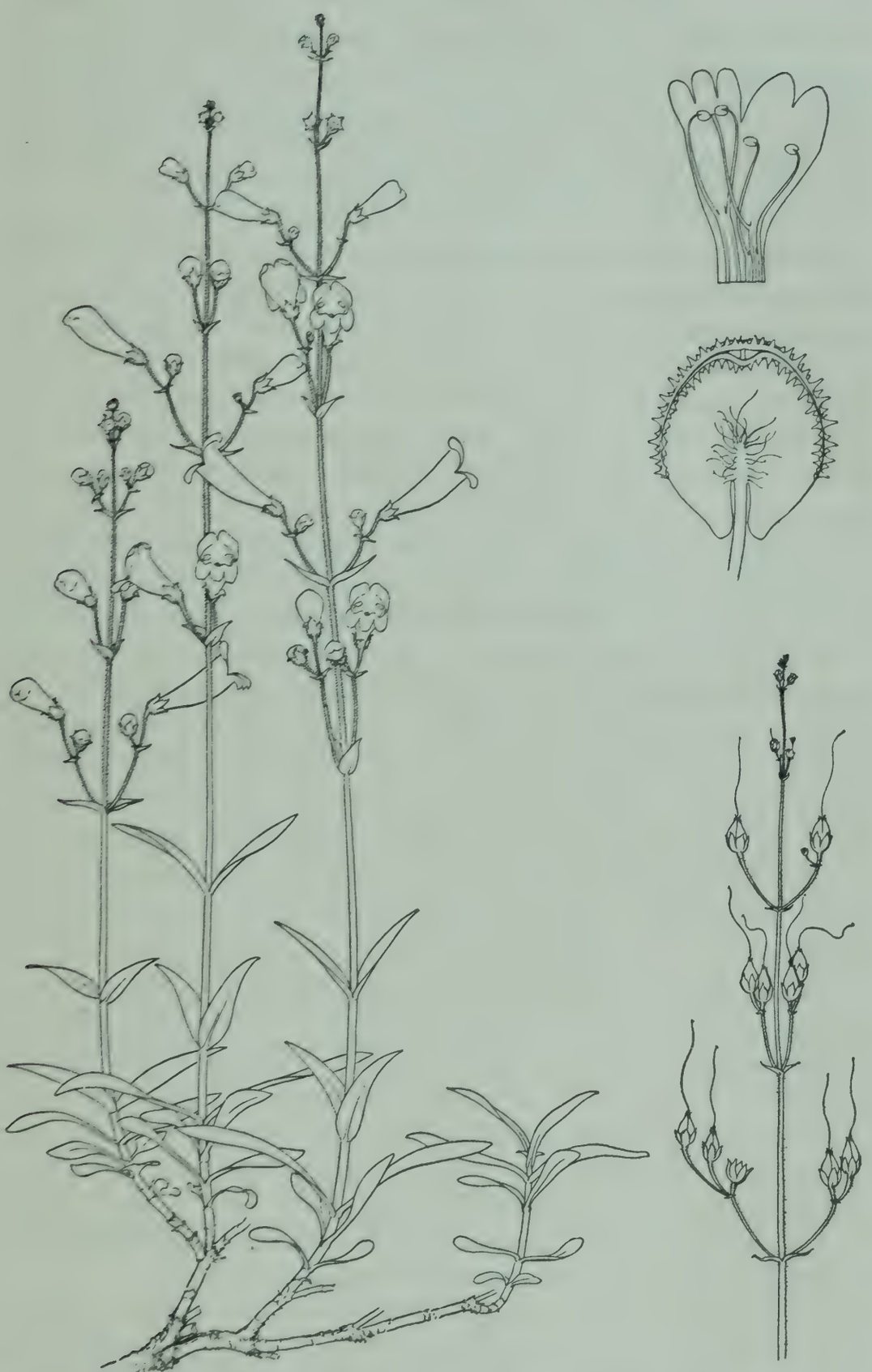


Fig. 13. *P. neotericus* Keck from the type collection. Habit and fruiting inflorescence × *ca.* ½; corolla opened longitudinally × *ca.* 1; anther × *ca.* 10.

(Jepson); Prattville, July 5, 1897, *Jones* (Po); 5 miles E. of Mineral, *Keck* 960 (Berlin, CA, CI, DS, G, Kew, Miss, Phila, Po, UC); Domingo Springs, *Keck* 967 (CI, DS, Phila); Camp Rodgers, Feather River Region, June 20, 1920, *Head* (CA). Sierra County: Cedar Glen, May 25, 1920, *Jones* (CA). Butte County: Humbug Summit, *Keck* 970 (Berlin, CA, CI, DS, G, Kew, Miss, Phila, Po, UC); Chaparral, *Keck* 971 (CI, DS, Miss, Phila, Po, UC); Jonesville, *Copeland* 193 (DS); Little Summit, *Heller* 11485 (CA, DS, G, UC).

Herbarium studies first suggested that this species had arisen through hybridization between *Penstemon laetus* and *P. azureus.* The collections studied showed considerable fluctuation in the characters indicating that recombinations and new combinations of the parental characters might still be occurring. No character was discovered in herbarium material through which this species differed from both parents, though its intermediate geographic position was noted. It was found that this material bore the characters of *P. laetus* and *P. azureus* about equally, so it was separated from both of them and considered as a new species. Subsequent field studies have shown that this material amply deserves the specific category, and in addition, other characters were discovered that had escaped notice when only herbarium material was studied. The species was found to be very constant and plentiful in southwestern Lassen County and northern Plumas County. In this region no representatives of *P. laetus* or *P. azureus* were seen, and *P. neotericus* did not exhibit the amount of variation to be expected from hybrid populations. Here, also, the corolla was very bright, mostly of the definite tri-colored aspect indicated. In northern Butte County, on the other hand, the flowers became more uniform in color, a dark blue-violet, which was very similar to the corolla coloring in *P. laetus leptosepalus,* found growing side by side with *P. neotericus* at Chaparral. At this location the two species were evidently crossing, for unmistakable hybrids were found among the parent species. Other field observations upon *P. neotericus* indicate an inflorescence more viscid than is common in *P. laetus,* foliage more white-glaucous than the blue-glaucous *P. azureus,* and buds bright yellow tipped with brownish which has not been observed in the yellow-budded *P. azureus,* and is different from *P. laetus* with its bluish purple buds that are sometimes pale yellow.

Field work has not changed the first opinion made in the herbarium—that this species is of hybrid origin. It is almost certain that if collections of *P. neotericus* were divided between the inflorescence and vegetative portion and distributed, the inflorescences would pass as undoubted *P. laetus,* the vegetative portions as typical of *P. azureus.*

Both of the supposed ancestral species border the range of *P. neotericus,* and there must have been ample opportunity for crossing between them particularly on the western border. Therefore I conclude that *neotericus* has arisen through hybridization between *laetus* and *azureus,* but that it no longer constitutes a hybrid population, having become a stable species over a considerable territory not now occupied by the supposed ancestral species. This invasion of a district not occupied by *laetus* and *azureus* has prevented backcrossing with those species except along the borders of its range where it meets them and this fact has doubtless aided in the establishment of a species uniform in its characters over large portions of its distribution.

12. **Penstemon azureus** Benth.

Penstemon azureus Benth., Pl. Hartw. 327, 1849.

Suffrutescent subshrub 2–5 (–6) dm. high: herbage light green, blue-glaucous, glabrous throughout: leaves dimorphous; basal narrowly oblanceolate to obovate (mostly linear in subsp. *angustissimus*), narrowed to a short petiole-like base, 1.5–6 cm. long, 2–10 (–20) mm. wide; upper cauline narrowly lanceolate or broader to oblong or ovate, sessile, mostly amplexicaul, noticeably widest or flaring at base, 1.4–6 cm. long, 4–15 (–20) mm. wide: peduncles appressed to main axis: calyx 3.5–6 mm. long; sepals ovate, oblong, or obovate, contracted abruptly to base of narrow mucronate or attenuate tip (the tip elongated in subspp. *parvulus* and *angustissimus*), the margins entire or erose, scarious: corolla deep blue-purple, with lilac tube, and purple or azure-blue lips, glabrous: lower pair of stamens slightly exceeding throat, upper pair ½–⅔ as long; anthers approximately cordate, as broad as long, dehiscent ½–⅔ the length of sacs, the teeth on line of dehiscence often in two ranks and conspicuous.

In the mountains, especially in openings of the chaparral, from southernmost Oregon to northern Tulare County, and to Trinity and Humboldt counties, California.

Key to the Subspecies of Penstemon azureus

A. Corolla 18–30 mm. long; anthers 1.75–3.25 mm. long.
  B. Basal leaves lanceolate but tapering from middle to base and apex, 2–5 mm. wide; sepals usually terminated by subulate tip 1–3 mm. long. 12*a*. **angustissimus**
  BB. Basal leaves oblanceolate to obovate, 4–20 mm. wide; sepals usually terminated by a cuspidate or mucronate tip less than 1 mm. long. 12*b*. **typicus**
AA. Corolla 14–20 mm. long; anthers 1.4–1.8 mm. long; sepals obtuse or acute, occasionally attenuate..... 12*c*. **parvulus**

12a. **Penstemon azureus** subsp. **angustissimus** (Gray) comb. nov.

Penstemon tenellus Kellogg, Proc. Calif. Acad. Sci. 1:56, 1855. Apparently belonging to this subspecies, the type material probably from near Placerville.

Penstemon azureus var. *angustissimus* Gray, Syn. Fl. 2[1]: 272, 1878.

Subshrub 3.5–6 dm. high: herbage glaucous, pale or yellow-green: basal leaves linear or lanceolate tapering to both base and apex, petiolate, 2–7 cm. long, 2–5 mm. wide; upper leaves increasing in basal width as they approach the inflorescence, lanceolate, acuminate, sessile, widest at base, 2–5 cm. long, 3–9 mm. wide: sepals oblong or obovate, extending into an abrupt subulate tip 1–3 mm. long: corolla 20–30 mm. long: anthers 2–3 mm. long.

At elevations of 500–800 m. in the Sierra Nevada foothills from Butte County to Madera County, also in western Glenn County, California. In Tuolumne County, found as high as 2200 m. near White Wolf. "Yosemite Valley, &c."

CALIFORNIA. Butte County: near Berry Creek Inn, *Keck* 451 (CI, DS, G, Geneva, Berlin, Po, UC). Nevada County: Grass Valley, *Heller* 8115 (DS, G, UC). Placer County: Colfax, *Jones* 3437 (CA, Po). El Dorado County: Sweetwater Creek, *Brandegee* (UC). Amador County: Jackson, *Mulliken* 114 (DS, Po, RM, UC). Calaveras County: Sheep Ranch, *Davy* 1616 (UC). Tuolumne County: White Wolf, July 1901, *Evans* (UC, plant rather matted, stems very woody, leaves crowded and small). Mariposa County: Yosemite Valley, *Bolander* 6312 (G, cotype) 1872, *Gray* (G, cotype). Madera County: Ahwahnee, *Jepson* 8407 (Jepson). Glenn County: Alder Spring, *Hall* V-894-D (CI).

12b. **Penstemon azureus** subsp. **typicus** nom. nov.

Penstemon azureus Benth., l.c. I have a photograph, fragment, and description of the type (*Hartweg* 313, serial 1879) taken at Bentham's herbarium, Kew, by H. M. Hall in 1928. I have also a photograph of a duplicate sheet of *Hartweg*, serial 1879, at Kew, not Bentham's herbarium. These show that the type is rather narrow-leaved. Quoting Hall: "Lower leaves very narrow; middle ones broad-lanceolate, acuminate, the base subcordate, 5–9 mm. wide." The duplicate sheet, mentioned above, and also represented at the Gray Herbarium, has very narrow leaves half again as long as the type and perhaps would best be referred to the subspecies *angustissimus*.

Penstemon glaucifolius Gray, Pacif. Rail. Rep. 6:82, 1857. Type from Fort Reading (about 10 miles southeast of Redding), California, collected by Newberry. A form with thicker, wider, more closely overlapping leaves than the type of *P. azureus*, and the bracts of the inflorescence are more than ordinarily leafy. As intimated by Gray, the presence of a bearded sterile filament is not a character

upon which named forms can be based in this group of the section. While no other example of the pubescent filament has been discovered by the writer in subsp. *typicus*, he has found it upon two occasions in subsp. *angustissimus*, and also, upon four collections of *P. heterophyllus* subsp. *purdyi*. Its appearance is considered a reversion to the ancestral type in this group of species, and the expression is noted to be variable within a single inflorescence. When it is found here, the beard is generally sparse but in one plant of *P. heterophyllus* from Mendocino County the staminode bore a dense beard. Evidently the bearded sterile filament may occur rarely in any of the species of this section in which they are normally glabrous.

Penstemon jeffreyanus Hook., Bot. Mag. t. 5045, 1858. A photograph and notes of *Jeffrey* 1116 in Hooker's herbarium at Kew, have been furnished me by H. M. Hall. This should be understood as the type as it was mentioned by Hooker and the garden specimen drawn for the plate has apparently not been preserved. Jepson, at Kew in 1906, took *Jeffrey* 1116 as the type, while Hall says of it: "—which I take as best representing the species." Hall notes additionally: "At Kew (Herb. Hook.) is an inflorescence labeled merely 'Hort. Veitch.' This has only one leaf and this is a bract on inflorescence: It is broad-ovate, broader than any in types of *azureus* or even in plate of *jeffreyanus*. But the piece probably was cultivated with the plant drawn." It is obviously better to consider *Jeffrey* 1116 as the type than this garden inflorescence. The Jeffrey specimen is of the large-leaved form frequently seen in collections from the upper Sacramento Valley. The largest pair of leaves on the single shoot are 12 mm. wide and 40 mm. long, and are oblong-elliptic as compared with the corresponding leaves on the type of *azureus* which are lanceolate. The Clear Creek from which the specimen came, is doubtless that a short distance to the west of Redding, Shasta County, California, and runs into the Sacramento River about five miles below that city. The obtuse leaves of *jeffreyanus* and the acute or acuminate leaves of *azureus* have long been the basis for specific or varietal distinction, but the accumulation of considerable material shows the futility of supporting such separation. The bulk of the material falls into neither category but into the intermediate leaf-shapes. When it is considered further that there is no geographic separation, there is no other choice than to hold these under one name.

Penstemon azureus var. *jeffreyanus* Gray, Bot. Calif. 1:561, 1876.

Penstemon heterophyllus var. *azureus* Jepson, Man. Calif. 917, 1925, as to synonymy.

Subshrub 2–5 dm. high: herbage blue-glaucous, occasionally gray- or yellow-green: basal leaves and those of sterile shoots oblanceolate to obovate, short-petiolate, 1.5–6 cm. long, 4–16 (–20) mm. wide; upper leaves of fertile shoots lanceolate or oblong to broadly ovate, sessile, those immediately below inflorescence widest at base, tapering to an acute or acuminate tip, or ovate becoming obtuse at tip, 1–4 cm. long, 6–15 mm. wide: sepals oblong or more often obovate, abruptly constricted to a cuspidate or mucronate tip, sometimes acuminate: corolla 20–30 mm. long: anthers 2.25–3.25 mm. long.

At moderate altitudes (1000–2300 m.) in Jackson and Josephine counties, Oregon, and in California from Del Norte to Trinity and Humboldt counties, and from Siskiyou County south to Placer County, recurring in Madera and adjacent Fresno counties. "In amnibus exsiccatis vallis Sacramento."

OREGON. Jackson County: Pilot Rock, Siskiyou Mountains, *Applegate* 5447 (DS). Josephine County: Rough and Ready Creek, *Wolf* 881, *Kildale* 5835 (DS); Waldo, *Kildale* 7907 (DS); ten miles south of Kerby, *Thompson* 4638 (DS). Curry County: trail, Collier Bar to Game Lake, *Leach* 2552 (UO). CALIFORNIA. Del Norte County: Gasquets, *Abrams* 8509 (DS, Po). Trinity County: Weaverville, 1915, *Junkans* (CA); South Yollo Bolley, July 25, 1897, *Jepson* (Jepson). Humboldt County: Lasseck Peak, *Goddard* 666 (UC). Siskiyou County: between Mt. Shasta City and Castle Lake, *Smith* 367 (CA). Shasta County: Castella, *Eastwood* 1365 (CA, G); Delta, *Eastwood* 11970 (CA); Ydalpom, *McAllister* 3 (CA, G); Fort Reading, *Newberry* (G, type of *P. glaucifolius* Gray). Tehama County:



Fig. 14. *P. azureus* subsp. *typicus* Keck. Anther × 10.

Red Bluff, June 1917, *Wickes* (CA). Butte County: Forest Ranch, *Bruce* 2412 (Po, DS). Sierra County: Webber Lake, Aug. 6–12, 1927, *Haley* (CA, Po). Nevada County: east of Emigrant Gap, *Keck* 423 (CI, DS, G, Geneva, Kew, Po, UC). Placer County: Donner Lake, *Heller* 6966 (DS, G, Po, RM, UC); Cisco, *Hall* 8702 (DS, G, Po, RM, UC). Madera County: North Fork, San Joaquin River, Aug. 18, 1895, *Congdon* (DS, UC). Fresno County: Lake Florence, vicinity of Huntington Lake, *Russell* 62, and 71 (DS); Big Creek, July 1915, *McDonald* (CA).

This subspecies is extremely variable and could be broken up into several smaller units for classification purposes if that were thought desirable. For instance, the first eight specimens cited could easily be referred to five different groups. The Pilot Rock collection resembles the majority of those from Shasta County, with thick leaves and green stems. The plants from Rough and Ready Creek are very robust, with thick, woody twigs, gray-glaucous foliage, and purplish stems. The collections from Waldo, and ten miles south of Kerby are quite different, retaining the robust habit but differing in their bright green foliage and stems, and deep purple peduncles and sepals. The Curry County collection strongly resembles subsp. *parvulus* in habit,

stature, and foliage, but all parts of the inflorescence are characteristic of *typicus*. The cited collection from Del Norte County is of a slender plant with lower leaves almost linear, and flowers about as small as those of *parvulus*, but it lacks the creeping habit, and the abundant, recurving basal leaves, with their characteristic folding along the midrib, of that subspecies. Apparently, in the general region represented by the above citations there occur all combinations of characters from those of subsp. *parvulus* to those of an exceptionally robust form. The Weaverville specimen is of another biotype, having small, narrow leaves, these well separated and bluish, and a long inflorescence with long, slender peduncles bearing large flowers. In southern Siskiyou County the material is dark green and thin-leaved with corollas of moderate size. Collections from there suggest the transition between *parvulus*, to the north, and the very robust *typicus* of Shasta County. Two other forms are recognizable in Shasta County, both of which are for the most part very thick-leaved. One, with the widest leaves, the extreme of which are ovate, and obtuse at the apex (*cf. Eastwood* 11970 and *McAllister* 3), is of a deep yellow-green color. The type of *P. jeffreyanus* was probably of such a biotype. The other form grades into this but typically has very glaucous and white, lanceolate or oblong, imbricated leaves; and it occurs from northern Shasta County to Butte County. In the latter county, all the material examined has been of this form. The collections from the high mountains in the region of the Nevada-Placer county line are possibly separable on the low habit and small basal leaves; while the collections seen from Tulare County might have been classed as subsp. *angustissimus*, to which they are very similar.

Ten forms, or biotypes have been pointed out from among the representative collections chosen for citation. Some are of more value than others, to be sure, but all are based on few characters of minor importance. The differences between the extremes are such as to cause much wonder that all are retained under one name. Intergrades, however, are found between these groupings throughout the subspecies. The question facing the classifier is whether the ten groups should receive names or whether all should be retained in one large aggregate. For the following reasons the ten are unnamed here: (1) the forms are not clear-cut from each other and so are hard to describe and identify; (2) naming them would not clarify the taxonomy of the species but would burden us with additional names;

(3) doubtless many more biotypes exist than have as yet been observed, and should be named as discovered to carry out the consistency of this classification; (4) few herbaria would have representatives of even a majority of these biotypes for comparison; (5) as far as this paper is concerned, the naming of these forms as subspecies would diminish the standard set in the treatment of other subspecies, and, it is thought, the treatment of these as quadrinomials would not serve a useful end.

The matter of these minor variations in this subspecies is given in some detail because it is a constantly recurring problem in the species of this genus as elsewhere in the plant kingdom. Cultural experiments upon *Penstemon* indicate that numerous fixed biotypes exist within many species, that are of a genetic nature rather than mere ecologic variations. Any species that contained a number of these would be large and its classification must then rest upon a utilitarian basis, for, from the genetic viewpoint, we might expect no end to the number of combinations presentable by nature.

12c. **Penstemon azureus** subsp. **parvulus** (Gray) comb. nov.

Penstemon azureus var. *parvulus* Gray, Syn. Fl. 2[1]:272, 1878.
Penstemon parvulus Krautter, Contr. Bot. Lab. Univ. Pennsylv. 3:193, 1908.
Penstemon jeffreyanus var. *parvulus* Jepson, Man. Calif. 917, 1925.

Perennial herb, woody at base, 2–3.5 dm. high, often creeping: herbage glaucous, deep green or gray-green: basal leaves narrowly to broadly oblanceolate or spatulate, petiolate, 1–3.5 cm. long, 2–5 (–8) mm. wide; upper leaves lanceolate, oblong, or narrowly ovate, semi-amplexicaul, 1–2.5 cm. long, 3–10 mm. wide: sepals lanceolate to oblong, elliptical or oval, obtuse or acute, often mucronate or attenuate: corolla 14–20 mm. long; anthers 1.4–1.8 mm. long.

Range discontinuous, the subspecies being found in the Siskiyou Mountains of Siskiyou County, California, at elevations of 1400–2500 m., and reappearing in the Sierra Nevada of southern Fresno and northern Tulare counties at high elevations, even to 3000 m. "Northern part of California, in mountains above Jackson Lake, at 8,000 feet, *Greene.*" (Siskiyou Mountains.)

OREGON. Jackson County: Buckhorn Peak, July 5, 1899, *Dudley* (DS). (This is probably the Buckhorn Mountain in Marble Mountains of west-central Siskiyou County, California.) CALIFORNIA. Siskiyou County: Shackleford Creek, *Butler* 1669 (DS, Po, RM, UC); Highland Mine, *Butler* 937 (UC); Salmon Summit, *Kildale* 5350 (DS); above Jackson Lake, *Greene* 1019 (G, type), 1021 (G); Mount Eddy, *Heller* 12485 (CA, DS, G). Fresno County: Horse Corral Meadow, *Dudley* 3166 (DS). Tulare County: Alta Peak, Sequoia National Park, *Grant* 1584 (UC); Kaweah River, *Dudley* 1726 (DS); Mineral King, *Hall & Babcock* 5352 (DS, UC).

The basal leaves and those of the sterile shoots do not fully expand laterally and so are usually folded along the midrib in herbarium material. These leaves also curve back so the outline of the pressed specimen is lunate. This is not distinctive of the subspecies, but is much more pronounced here, becoming striking in the southern material.

The peculiar distribution of this subspecies is paralleled in various other species of California plants as pointed out by Jepson[6], who indicates its connection with the geologic history of the region.

A noteworthy variant is represented by a collection from the Siskiyou Mountains of Jackson County, Oregon, *Cusick* 2939*b* (UO), in which the upper cauline leaves average less than 1 cm. long, the others being proportionally small. The collection is in fruit, but one withered flower shows it is referable to this subspecies rather than *typicus*. The small stature of the plant (12–15 cm.) suggests it might be of a new subspecies, if the collection is representative of a considerable colony in this region rather than merely an isolated aberrant individual.

Relationships of Penstemon azureus

This species may best be considered as derived from *Penstemon laetus*, for the anthers, sepals, and corollas show a greater separation from the Great Basin species than do these organs in *P. laetus*, but the affinity of *P. azureus* to the latter species is marked. The connection is most evident through *P. azureus angustissimus* and *P. laetus typicus* or a similar form for in these the similarities in leaf- and sepal-shape is most evident. The possibility exists that *P. azureus typicus* developed directly from *P. laetus* and, in turn, gave rise to subsp. *angustissimus*, which, however, regained some of the *laetus* characters through crossing with that species. Since the latter hypothesis appears more speculative, it is proposed here that subsp. *angustissimus* developed from *laetus* and in turn gave rise to *typicus*. Undoubtedly *P. azureus parvulus* is connected with and probably a development from *P. azureus typicus*, for there are intermediates, in southern Siskiyou County and the Siskiyou Mountains, that almost close the gap between them.

---

[6] Manual of the Flowering Plants of California 11, 1925.

13. **Penstemon heterophyllus** Lindl.

Figures 15–16

Penstemon heterophyllus Lindl., Bot. Reg. 22:t. 1899, 1836.

Suffrutescent subshrub 3–15 dm. high: herbage grayish, yellowish, or bluish green, rarely glaucous, glabrous or puberulent throughout: leaves all of one kind, narrowly linear to lanceolate, or the basal narrowly oblanceolate, 2–10 cm. long, 2–8 mm. wide; upper cauline sessile or half-clasping, but not noticeably flaring or widest at base: peduncles appressed to main axis: calyx 4–6 mm. long; sepals lanceolate to ovate, rarely obovate, usually acute to attenuate at apex, sometimes contracted abruptly to base of acuminate or attenuate tip, the margins entire or erose, hyaline only basally if at all: corolla rose-violet, with blue or lilac lobes, glabrous: lower pair of stamens equaling or slightly exceeding throat, upper pair ½–⅔ as long; anthers typically sagittate, *ca.* ⅔ as wide as long, dehiscent ⅗–⅘ the length of sacs, the teeth on line of dehiscence often in two ranks and conspicuous.

In the Coast Ranges of California from southern Humboldt and Trinity counties to San Diego County, and in the foothills bordering the Sacramento Valley.

Key to the Subspecies of Penstemon heterophyllus

A. Herbage of inflorescence puberulent; sepals lanceolate to ovate.
  B. Leaves 3–6 (–9) cm. long, 3–6 (–9) mm. wide, rarely fascicled, usually lax at base of flower-stalks; sepals usually glabrous.
    C. Teeth on anther-orifice smaller, usually much less than and rarely exceeding 0.25 mm. long. California.....13*a*. **purdyi**
    CC. Teeth on anther-orifice larger, as much as 0.40 mm. long. New Mexico. .....13*b*. **spinulosus**
  BB. Leaves 2–4 cm. long, 2–3 mm. wide, usually fascicled, becoming crowded at base of flower-stalks; sepals usually puberulent.....13*c*. **australis**
AA. Herbage of inflorescence glabrous; sepals mostly oblanceolate to obovate; leaves 2–3 (–5) cm. long, 2–4 mm. wide.....13*d*. **typicus**

13a. **Penstemon heterophyllus** subsp. **purdyi** subsp. nov.

Penstemon heterophyllus α Hook. et Arn., Bot. Beech 376, 1840 (in part). "Sepalis ovatis acuminatis."

Penstemon heterophyllus β Hook. et Arn., l.c. (in part). "Sepalis orbiculari-ovatis cuspidatis." This is the most common form in *typicus*, while α Hook. et Arn. is most common in this subspecies and *australis*. Neither trinomial deserves further recognition as the sepal characters in this species vary from locality to locality with no definite trend.

Penstemon heterophyllus var. *azureus* Jepson, Man. Calif. 917, 1925, as to description, not as to synonymy. (Not *P. azureus* Benth.) Jepson's category embraces the Sierran foothill material of this subspecies.

Frutex, 3–3.5 dm. altus, plerumque omnino puberulentus; foliis anguste oblongis, basi in petiolis gradatim attenuatis, apice obtusis aut rotundatis, rare fasciculatis, 4–6 cm. longis, 4–6 mm. latis, e basi caulis ad inflorescentiam aequidistante positis; sepalis glabris, lanceolatis vel ovatis, ad apicem acutis vel acuminatis.

This description is taken from the type specimen. Consideration of the isotypes and abundant material representative of this subspecies requires that it be supplemented as follows: shrub 2.5–7 dm. high: leaves in pairs, rarely in fascicles due to development of the lateral buds, often linear and acute, 2.5–6 (–9) cm. long, 3–6 (–9) mm. wide; sepals usually glabrous, occasionally puberulent.



Fig. 15. *P. heterophyllus* subsp. *purdyi* Keck. Anther × 10.

Infrequent in the Sierra foothills of California from Butte County to Placer County (doubtfully as far south as Yosemite Valley), and abundant in the North Coast Ranges from southern Humboldt and Trinity counties to San Benito County at elevations of 100–1600 m.

Type: Mount Hamilton, Santa Clara County, California, April 1903, *A. D. E. Elmer* 4832 (Dudley Herbarium of Stanford University, No. 68695; isotypes CA, Po, UC).

CALIFORNIA. Butte County: Berry Canyon, *Heller & Brown* 5482 (DS, G, Po); Rock Creek, 7 miles N. of Chico, *Heller* 13926 (UC, distributed in the topotype sets from Dudley Herbarium, Stanford University, as topotype of *P. azureus* Benth.). Glenn County: 5 miles E. of Newville, *Heller* 11428 (CA, DS, G, UC). Colusa County: west of Leesville, *Heller* 13118 (CA, DS, G). Sutter County: West Butte, *Ferris* 6362 (DS). Yuba County: Los Vergils, *Eastwood* 10554 (CA).

Placer County: 5 miles W. of Colfax, *Heller* 12748 (CA, DS, G). Trinity County: North Fork Eel River, *Goddard* 642 (UC). Humboldt County: Garberville, *Kildale* 1935 (DS). Mendocino County: Laytonville, *Abrams* 8214 (DS, Po); Potter Valley, *Eastwood* 12729 (CA). Lake County: Kelseyville, *Baker* 3089, 3091 (G, Po, UC). Napa County: Howell Mountain, *Tracy* 1486 (UC). Marin County: Mount Tamalpais, *Eastwood* 11357 (CA). Contra Costa County: Mount Diablo, *Baker* 2872 (Po). Santa Clara County: Hall's Valley, *Pendleton* 831 (Po, UC). San Benito County: Griswold Creek, *Abrams & Borthwick* 7945 (DS, Po).

It is a pleasure to name this subspecies in honor of Mr. Carl Purdy, of Ukiah, California, who has recognized for many years that this was distinct, and who introduced one of its forms to the horticultural trade as the "California Blue Bedder."

13b. **Penstemon heterophyllus** subsp. **spinulosus** (W. & S.) comb. nov.

Penstemon spinulosus Wooton & Standley, Contr. U. S. Nat. Herb. 16:173, 1913.



Fig. 16. *P. heterophyllus* subsp. *spinulosus* Keck. Anther × 10.

Like subsp. *purdyi* in all characters, as far as known, except teeth margining orifice of anther stout, subulate, often curved, not crowded, as much as 0.40 mm. long.

Known only from the type collection, made in the Santa Magdalena Mountains of New Mexico, in June 1881, by G. R. Vasey. Type, in the U. S. National Herbarium, kindly sent for my inspection, by Dr. W. M. Maxon.

13c. **Penstemon heterophyllus** subsp. **australis** (M. & J.) comb. nov.

Penstemon heterophyllus var. *australis* Munz and Johnston, Bull. So. Calif. Acad. Sci. 23:40, 1924.

Shrub 3–5 dm. high, puberulent almost throughout, usually densely so: leaves linear or narrowly lanceolate, tapering to base and apex, usually acute, in fascicles due to development of lateral buds, more crowded toward base of stem, 2–4 (–5) cm. long, 2–3 (–5) mm. wide: sepals lanceolate to narrowly ovate, acute or acuminate, usually puberulent, occasionally glabrous.

Common in the chaparral belt of the foothills and mountains of coastal southern California, from northern Santa Barbara County almost to the Mexican border; local in Monterey County; ranging from 100–1800 m. elevation. "Claremont, California, *Baker* 4778."

CALIFORNIA. Monterey County: Tassajara, June 11, 1901, *Dudley* (DS); east of Twin Peaks, Santa Lucia Mountains, Aug. 1903, *Dudley* (DS). Santa Barbara County: Cuyama River, April 28, 1926, *Jones* (CA, DS, Po, UC). Ventura County: Fillmore, *Hall* 3110 (DS, Po, RM, UC). Los Angeles County: Elizabeth Lake, *Parish* 1885 (DS, UC); Claremont, *Baker* 4778 (Po, type). San Bernardino County: Mill Creek, *Parish* 5055 (DS, Po). Orange County: Santiago Peak, *Munz* 7748 (Po, UC). San Diego County: Cuyamaca Lake, *Munz & Harwood* 7210 (G, Po, UC); Descanso, *Eastwood* 9089 (CA).

13d. **Penstemon heterophyllus** subsp. **typicus** nom. nov.

Penstemon heterophyllus Lindl., l.c. I have been kindly furnished notes taken by Jepson in 1906, Hall in 1928, and Sprague in 1930 upon the plant collected in California by Douglas in 1833. This is in the Bentham herbarium at Kew and should doubtless be regarded as the type. There is no garden specimen of the time preserved at Kew, and I don't know whether there is one in Lindley's herbarium. My efforts to have a possible type unearthed at the Lindley herbarium at Cambridge have to date been fruitless. Dr. Sprague was kind enough to furnish me with a photograph and fragments of the Douglasian plant at Kew which are deposited in the working collection of the Carnegie Institution. These data indicate that this specimen has at most minutely puberulous stems and pedicels, glabrous or minutely ciliolate leaves, and glabrous, oblong-obovate sepals with broad shoulders and abruptly contracted to lanceolate tips.

Penstemon heterophyllus α Hook. et Arn., l.c. (in part).

Penstemon heterophyllus β Hook. et Arn., l.c. (in part). See discussion under these in synonymy of subsp. *purdyi*.

Penstemon leucanthus Greene, Pitt. 1:72, 1887. Aside from the height, recorded as from 4 to 6 feet, this seems to be merely an albino form of the species. I have not seen the type, from the San Rafael Mountains, Santa Barbara County, California, June 1887, *Spence*. Subsequent thorough botanizing of this area has not rediscovered the form to my knowledge.

Shrub 3–5 dm. high, glabrous throughout or occasionally minutely puberulent at base of stems, the pedicels and ventral side of sepals often granular: leaves linear, tapering to base and apex, often

glaucous, usually fasciculate, 2–3 (–5) cm. long, 2–4 mm. wide: sepals mostly oblanceolate to obovate, abruptly constricted to the acuminate or subulate tip in northern material, glabrous.

Frequent in the Coast Ranges of California from northern Lake County to the San Gabriel Mountains, Los Angeles County; rare in San Diego County; occurring at elevations of 100–1600 m. "A native of California where it was collected by Mr. Douglas."

CALIFORNIA. Lake County: Mount Hull, *Hall* 9563 (UC); Hough's Springs, *Heller* 12377 (CA, DS, G). Sonoma County: between Knight's Valley and Mark West Springs, *Heller* 5790 (DS, G, Po, RM). Alameda County: Mocho Creek, *Elmer* 4394 (DS, Po, UC. One specimen finely puberulent, otherwise typical, CA). Santa Clara County: Mount Hamilton, May 19, 1923, *Lang* (DS, Po). San Benito County: Tres Pinos Creek, *Abrams & Borthwick* 7995 (DS). Monterey County: Tassajara Hot Springs, *Elmer* 3394 (DS, Po). San Luis Obispo County: Atascadero, *Guirado* 518 (UC). Santa Barbara County: Sisquoc, *Baker* 37 (UC). Ventura County: Sespe Creek, *Abrams & McGregor* 164 (DS, G, Po). Los Angeles County: Mount Gleason, *Elmer* 3707 (CA, DS, G, Po, UC). San Diego County: Cuyamaca Lake, *Wiggins* 3155 (DS).

Relationships of Penstemon heterophyllus

At this time it is impossible to state whether *Penstemon heterophyllus* was derived from *P. laetus,* or *P. azureus,* or both. Its connections with these two possible ancestors appear to be equally close. If *laetus* is considered the ancestor, the closest connections are doubtless between *laetus sagittatus* and *heterophyllus purdyi.* These are in close proximity in Humboldt County and are very similar in all respects except the glandular-pubescent inflorescence of the former. The same subspecies of *heterophyllus* occurs near *laetus typicus* in the Sierran foothills, but the latter is morphologically further removed from *heterophyllus purdyi* than is *laetus sagittatus* because it has broad anthers and large, soft, hairy leaves, the upermost of which are broadly lanceolate. If *azureus* is considered the ancestral species, it would doubtless be assumed that the connection existed between *azureus angustissimus* and *heterophyllus typicus,* for only a few technical characters serve to separate these, and only one, namely, the shape of the leaves just below the inflorescence, is found solely in one and not in the other. But *heterophyllus typicus* has the characteristic sepals of the broad-leaved *azúreus typicus* rather than those of *azureus angustissimus.* Such broad-shouldered sepals are most prominent in the Lake County material of *heterophyllus typicus,* which may be significant in that this district is the nearest approach of this sub-

species to *azureus typicus.* The latter is not known to occur in Lake County although it occurs farther north. But since *heterophyllus typicus* and *azureus typicus* are quite different in leaf-characters, and since, in addition, *heterophyllus typicus* is geographically separated from *azureus angustissimus,* such a derivation does not seem as probable as that of *heterophyllus* through its subspecies *purdyi* from *laetus sagittatus.*

Garden experiments have given positive indication of the stability of the characters employed to distinguish subspecies and species here. A plant of *P. heterophyllus typicus* has been growing for seven years in a garden fully exposed to the sun, and it has not gained any hairs nor changed the shape of its leaves and sepals. Five plants of *P. azureus angustissimus* have been grown at 30 m. and another set from the same roots have been grown at 1500 m. altitude without altering their subspecific characteristics. The rather subtle differences in leaf-shape were apparent when the two species were grown side by side. Seedlings of the three California subspecies of *heterophyllus* have been growing side by side for two years without any apparent masking of their key differences.

If *purdyi* is considered as the phylogenetically oldest subspecies of *P. heterophyllus,* there is little difficulty in assuming that the remaining subspecies were derived directly from it. Possibly *typicus* was separated from *purdyi* before the outside influence of *azureus* was felt. This would explain the slight differences between *typicus* from north-central and from southern California. The more arid conditions of the southern part of the state are perhaps responsible for the increased puberulence, and the shortened internodes with consequent crowding and fasciculation of the leaves of *australis.* It cannot be said that *spinulosus* has any discernable strong morphologic characters on which to stand. But it should be recalled that the only known collection came from a little-frequented portion of New Mexico so many years ago that it would seem certainly to be native in that region rather than an introduction by man. This type specimen is well faded and scarcely complete enough to assure a complete comparison with *purdyi.* No California collection has been observed to have anthers directly comparable to those of *spinulosus,* so that the difference which at first appears trivial seems to be definite. Other characters have failed to disclose themselves but may be noted when the subspecies is re-collected in New Mexico. Apparently this is a migrant from California at an early time when the desert region was a less

imposing barrier to such a migration. At all events, *spinulosus* connects definitely with *heterophyllus,* of California, rather than with any of the Utah or Great Basin species of the section.

14. **Penstemon purpusii** Brandegee

Penstemon purpusii Brandegee, Bot. Gaz. 27:455, 1899.

Perennial herb 1.0–2.0 dm. high; older branches spreading over ground and rooting, newer shoots decumbent or ascending: herbage gray-green, not glaucous, canescent, inflorescence densely glandular-pubescent: leaves dimorphous, equally distributed along stems, soft, mostly entire but some shallowly dentate or serrate; lower oval to rotund with petiole half as long as blade; upper oval, oblanceolate or lanceolate, sessile, lower and upper 10–20 mm. long: inflorescence a crowded panicle, usually short, 3–8 (–15) cm. long; peduncles 1–3-flowered, appressed to main axis; pedicels very short: calyx 5–10 mm. long; sepals linear-lanceolate to broadly oval, attenuate to broadly obtuse at apex, not truncate, entirely herbaceous, margins entire: corolla violet shading to blue on tube, the buds violet, 20–30 mm. long, 5–7 mm. wide at throat when pressed, glandular-pubescent without, glabrous within, rather abruptly dilated into an ample throat twice as long as tube, slightly constricted at orifice; lower lip slightly exceeding upper, *ca.* 5 mm. long, both diverging moderately: lower pair of stamens reaching orifice, upper pair nearly as long; filaments glabrous, the sterile one dilated and flattened at the glabrous tip; anthers saggitate but truncate at the very tip, bowed, 2.5–2.8 mm. long, 1.5 mm. wide, hirsute at sinus, dehiscent ¾ the length of sacs, the subulate white teeth on line of dehiscence not over 0.12 mm. long: capsule ovate, 8–13 mm. long, scarcely exceeding sepals: seeds few (19 in one typical capsule), wrinkled, irregular, average 2 mm. long, the seed-coat cinereous.

A species of restricted distribution, having been found only in the North Coast Ranges, California, from southern Trinity County to northern Lake County, at 1500–2400 m. elevation. "Snow Mountain, California, above 7000 feet altitude, *Dr. C. A. Purpus,* July 1894, nos. 1157, 1259."

CALIFORNIA. Trinity County: South Yollo Bolly, July 25, 1897, *Jepson* (Jepson), Sept. 1916, *Merriam* (CA). Mendocino County: Buck Rock Ridge, Forest Reserve, *Eastwood* 15290 (CA). Lake County: Mount Hull, *Hall* 9561 (UC); Mount Sanhedrin, *Hall* 9461 (G, UC), 9472 (UC), *Heller* 5948 (DS, G); Snow Mountain, *Purpus* 1157, 1259 (UC, types), Aug. 24, 1892, *Brandegee* (UC).

This species seems much like *P. laetus sagittatus.* The similarities are: pubescent herbage; glandular-pubescent inflorescence; sepals of similar size and shape; corolla of similar shape even to the slightly constricted orifice, and similar in size and color; sagittate anthers dehiscent *ca.* ⅗ the length of sacs; and numerous minor similarities. The differences may be expressed in parallel columns as follows:

Penstemon purpusii	*Penstemon laetus sagittatus*
1. Low plants; branches decumbent or ascending.	1. Tall plants; branches erect.
2. Herbage canescent, densely set with short white hairs.	2. Herbage finely puberulent, with white hairs of microscopic length, to nearly glabrous.
3. Leaves mostly entire, some shallowly dentate or serrate.	3. Leaves all entire.
4. Lower leaves oval to rotund, with petiole half as long as blade.	4. Lower leaves linear to oblanceolate, petiole not well defined.
5. Peduncles appressed to main axis of inflorescence.	5. Peduncles divergent from main axis of inflorescence.
6. Lobes of upper lip of corolla much less deeply cleft than those of lower lip.	6. Lobes of upper and lower lips of corolla *ca.* equally cleft.

The geographic distribution of the two species lends support to the supposition that *purpusii* has a close phylogenetic connection with *laetus sagittatus,* for, though the two are not known to intermingle at present they may well have done so in the past as they are but some 50 miles apart at comparable elevations.

Penstemon heterophyllus is less closely related to *purpusii,* for in addition to the differences cited above for *laetus sagittatus,* the inflorescence is not glandular and the corolla is more widely gaping.

15. **Penstemon diffusus** Lindl.

Penstemon diffusus Lindl., Bot. Reg. 14:t. 1132, 1828. The name taken from Douglas' Journal ined. The type, doubtless in Lindley's herbarium, has not been seen; but I have a photograph of a Douglas specimen in Bentham's herbarium labeled "Limestone rocks at the Grand Rapids. Dougl." Hall noted at Kew, "The spm. in Hb. Hook. is the same"—as the one in Hb. Benth.—"and the label adds '148 miles from the ocean'." Probably these sheets are not of the type collection.

Penstemon serrulatus Hook., Fl. Bor. Am. 2:95, 1838. The name taken from Menzies' manuscript. Type from the northwest coast of America where it was collected by Menzies. I have a photograph of a specimen in Hooker's herbarium labeled in Hooker's hand, "Penstemon serrulatus. Menz. A. M." This sheet is undoubtedly the type and is typical of *P. diffusus.* Also the description shows that *serrulatus* is referable to *diffusus.*

Penstemon argutus Paxt., Mag. Bot. 6:271, 1839. I have not seen this publication, nor have I a reference to any type, but the Kew Index lists the name as doubtfully the same as *P. diffusus.* Two sheets of garden specimens at Gray Herbarium labeled *P. argutus,* appear to be hybrids between *P. diffusus* and *P. richardsonii.*

Subshrub 3–7 dm. high: herbage often glabrous below, usually puberulent above, particularly on stems and within inflorescence: leaves subentire to irregularly serrate, dentate, or shallowly laciniate, often with undulate margins, 2–9 cm. long, 6–45 mm. wide; basal broadly lanceolate, elliptic, or spatulate, subsessile or usually with a petiole ⅓–½ the length of blade; upper cauline broadly lanceolate to cordate, sessile or clasping: inflorescence a narrow thyrsus of 1–5 verticillasters, the lower of these long-peduncled and well separated, the upper crowded; peduncles usually appressed to main axis: calyx 6–11 mm. long; sepals linear-lanceolate to ovate, entirely herbaceous, the margins becoming ciliolate, usually entire but frequently laciniate on wider sepals: corolla deep blue to dark purple, 16–23 mm. long, glabrous without and sometimes pubescent within at base of lower lip: lower pair of stamens reaching well into lip, upper pair extending to summit of throat; filaments glabrous, the sterile one yellow-bearded for outer ½ its length; anthers 1.3–1.6 mm. long: capsule 6–8 mm. long, somewhat exceeding the appressed sepals: seeds 1.0–1.5 mm. long.

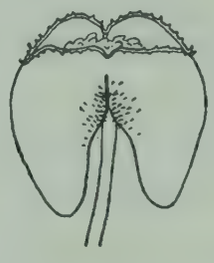


Fig. 17. *P. diffusus* Lindl. Anther × 10.

Frequent from central British Columbia and Vancouver Island to northwestern Oregon, mostly west of the crest of the Cascade Mountains, at elevations up to 1800 m. "Native of open grounds and banks of streams in the districts around the mouth of the Columbia River, where it was found abundantly by Mr. Douglas."

BRITISH COLUMBIA. Revelstoke, *Shaw* 904 (G); Chilliwack Valley, *Macoun* 54492 (G). Vancouver Island: Beaufort Range, Alberni, *Carter* 365 (G).

WASHINGTON. Whatcom County: Glacier, *Mason* 3827 (CI). Clallam County: Olympic Mountains, *Elmer* 2585 (DS). Chelan County: Bridge Creek, July 11, 1911, *Jones* (DS, Po, UC). Pierce County: Nisqually Checking Station, Mount Rainier, *Abrams* 9214 (DS, Po, RM). Yakima County: Goat Mountains, *Allen* 129 (DS, G, Po, RM, UC). OREGON. Hood River County: along Hood River, *Heller* 10111 (DS); Cascade Locks, *Keck* 335 (CI, UC). Multnomah County: Rooster Rock, May 26, 1885, *Henderson* (DS). Clackamas County: Clackamas River, July 1894, *Howell* (UC). Lane County: South Fork of McKenzie River, *Henderson & Patterson* 12763 (UO).

As pointed out in the introduction, *Penstemon diffusus* is considered the primitive member of the following group of species, and it appears to be closely connected with *P. ovatus* of the section *Graciles*. *Penstemon diffusus* and *P. ovatus* superficially resemble each other very closely in habit, shape and cut of leaf, color and size of corolla,

arrangement of inflorescence, and bearding of sterile filament. Also the distributional ranges of the two overlap. *Penstemon pruinosus* is but little further removed from *P. diffusus* being a pruinose-puberulent species with well-exserted corollas.

This species does not appear to develop striking variants. Probably the most important of its variations are in the shape and margin of the calyx-lobes. From a small, entire, lanceolate calyx-lobe, there is a progression to a large obovate one, abruptly constricted to the base of the acuminate tip, and with margins serrate to laciniate. This amount of variation is noted in different parts of the range of the species and apparently its occurrence is not limited geographically.

As an example of the modification obtainable in certain characters of this species and the stability of others, this bit of experimental evidence is presented. A plant, dug at Cascade Locks, Oregon, was propagated by root-cuttings. One portion of this individual was set out in a half-sunny situation at Mather, Tuolumne County, California, where the elevation is 1500 m., while anther portion was placed in a full-sun garden at Stanford University, elevation 30 m. The experimental results may be charted as follows:

	At Stanford	At Mather
Date of full bloom	July 1, 1929	September 1, 1929
Average height of flower-stalks	5.5 dm.	4 dm.
Length of typical leaf at base of inflorescence	9 cm.	3 cm.
Width of same	5 cm.	1.4 cm.
Length of typical inflorescence	37 cm.	11 cm.

Minor differences were observed such as intensification of the herbage- and flower-color, length of internodes, diameter of stems, etc., while no significant differences were observed in the sepal-shape, corolla-size, bearding of the sterile filament, and anther-size. Demonstration of such variation within a single clone should lead to caution in assuming that the small, slender, mountain forms of this species are of distinct biotypes from the luxuriant plants of the moist lowlands.

16. **Penstemon venustus** Lindl.

Penstemon venustus Lindl., Bot. Reg. 16:t. 1309, 1830. The name taken from Douglas in the herbarium of the Horticultural Society of London.

Penstemon amoenus Kunze, Linnaea 16:littbl. 107, 1842. The reference has not been read by me, but the species is generally referred to *venustus* by authors.

Penstemon suffruticosus Benth., in DC. Prod. 10:330, 1846. This Douglasian name is described under synonymy of *venustus* with no localities mentioned. I have a photograph from Hooker's herbarium of typical *venustus* labeled: "Penstemon suffruticosus in the gravelly channels of rivulets near the Blue Mountains. Abundant near the source of the Wallawallah river, Douglas." According to Hall, "In Hb. Benth. is a duplicate with fewer data." I judge this latter specimen must stand as the type.

Subshrub 3–8 dm. high: herbage glabrous except for lines of puberulence extending up stems from leaf-axils, the inflorescence glabrous: leaves evenly finely and sharply serrulate or toothed, these teeth often pungent and uncinate, 2–12 cm. long, 3–35 mm. wide; basal lanceolate and widest well above base to elliptic or oblong, sessile; upper cauline narrowly lanceolate to lance-ovate: inflorescence a spike-like thyrsus, seldom open; peduncles appressed to main axis: calyx 3–6 mm. long; sepals lanceolate, ovate, or obovate, the margins scarious, entire to erose or shallowly toothed: corolla bright blue, deep blue-purple, or violet, 20–32 mm. long, glabrous without and within, the lobes ciliate: lower pair of stamens reaching summit of upper lip, upper pair reaching summit of throat; filaments bearded with long white hairs for short distance from tip, the sterile one white-bearded particularly on the margins of the tip; anthers 1.6–2.1 mm. long: capsule 6–9 mm. long, mostly twice as long as appressed sepals: seeds 1.25–2.5 mm. long.



Fig. 18. *P. venustus* Lindl. Anther × 10.

Rather frequent in the mountains from north-central Idaho to the Wallowa and Blue Mountains of Oregon and southernmost Washington, at 750–2000 m. elevation. "Found by Mr. Douglas in the dry channels of rivers among the mountains of North-west America."

IDAHO. Shoshone County: Elk Creek, *Abrams* 812 (DS, UC). Idaho County: Craig Mountains and S. Clearwater, June 21–27, 1894, *Henderson* (RM). Nez Perces County: Lake Waha, *Heller* 3327 (DS, Po, UC). Washington County: Middle Valley, *Jones* 6494 (Po). WASHINGTON. Asotin County: Anatone, *Applegate* 6455 (DS).

Walla Walla County: Waitsburg, *Horner* B384 (G). OREGON. Wallowa County: Wallowa, *Thompson* 4819 (DS); Wallowa Mountains, *Keck* 369 (CI, DS, UC). Union County: Elgin, *Thompson* 4837 (DS). Umatilla County: Meacham, *Keck* 347 (Berlin, CA, CI, DS, G, Geneva, Kew, Miss, Phila, Po, UC).

The closest connections of *P. venustus* seem to be with *P diffusus*, and as both are essentially mountain species, the former may be considered a migrant to the interior from the coastal slopes of the Cascades. *Penstemon venustus* resembles *diffusus* in habit, general shape of the leaves, flowers, and sepals, and in that it has not developed, or has lost all glandular-pubescence. Many characters of *P. venustus* may be due to the environment, such as the thick, pithy stems, yellow-green herbage, longitudinal bands of puberulence on the stems, often pungently toothed leaves that are thickened at the margins, and the scarious-margined sepals. On the other hand there are many differences, such as ciliate corolla-lobes and bearded filaments, that are not easily ascribable to the immediate effect of a different climate, and, accordingly, indicate that the separation between these species has been a long one.

Herbarium material indicates a uniformity in the species, but it is noticeable that Oregon specimens are the more verdant while those from the drier hills of Idaho are more yellow, and their narrower leaves sharper-toothed.

17. **Penstemon richardsonii** Lindl.

Penstemon richardsonii Lindl., Bot. Reg. 13:t. 1121, 1827. Lindley took the name from "Douglas Journal, &c ined." Type not seen; probably in Herb. Lindley. Photo of Douglas specimen in Bentham's herbarium I have, the label reading: "Rocks of the Great Falls on the Columbia, and Falls on the River Multnomah. 1825." Hall notes: "At Kew there are several other sheets similar to this, some coll. Douglas, some from gardens."

Penstemon rivularis Trautv., Bull. Sc. Acad. Petersb. 5:345, 1839. The name credited to Douglas. A nomen nudum, referred to *richardsonii* by authors. No way to place this without seeing type.

Subshrub 2–8 dm. high: herbage almost glabrous to densely canescent, the inflorescence glandular-pubescent: leaves coarsely but acutely serrate to pinnately parted, the lobes again parted or toothed, narrowly lanceolate to narrowly ovate in outline, 2–8 cm. long, 8–20 mm. wide; basal short-petiolate; upper cauline sessile (at least those just below inflorescence): inflorescence seldom a raceme, usually a thyrsus or open panicle, simple to much-branched; peduncles usually divergent from main axis: calyx 4–7 (–9) mm. long; sepals lanceolate to broadly ovate, entirely herbaceous or the margins very narrowly

hyaline, entire: corolla pink to rose-lilac or bluish, the throat prominently striped within, (15–) 18–30 mm. long, usually glandular-pubescent without, usually glabrous within or with few long white hairs at base of lips: lower pair of stamens included in lip, upper pair very nearly as long; filaments glabrous, the sterile one yellow-bearded toward tip, rarely glabrous; anthers 1.3–1.8 mm. long: capsule 6–9 mm. long, somewhat exceeding the appressed sepals: seeds 1.25–1.75 mm. long.

Frequently on semi-arid hillsides from northeastern Washington, adjacent British Columbia, and north-central Oregon westward to the eastern slopes of the Cascade Mountains, at elevations of 350–1000 m. ". . . . found by Mr. Douglas in the north-western territories of North America, growing on bare dry rocks, in the vicinity of the Columbia and its branches."

BRITISH COLUMBIA. Similkameen River, *Macoun* 76763 (G).

WASHINGTON. Spokane County: Spokane, *Keck* 392 (CI, DS, Po, UC). Douglas County: Egbert Spring, *Sandberg & Leiberg* 345 (CA, G, UC). Chelan County: Tumwater Station, *Otis* 840 (CA). Kittitas County: Ellensburg, *Elmer* 405 (Po, RM). Skamania County: Cape Horn, *Suksdorf* 2319 (G, UC). OREGON. Umatilla County: Milton, *Brown* 44 (UC). Sherman County: De Moss Springs, *Peck* 9935 (DS). Wasco County: Tygh, *Abrams* 9532 (DS, Po, RM). Hood River County: Hood River, *Keck* 312 (Berlin, CA, CI, DS, G, Kew, Po, UC). Multnomah County: Wah-Kee-Na Falls, Columbia Gorge, *Abrams* 9312 (DS, Po). Clackamas County: Oswego Lake, *Nelson* 2758 (DS, G). Grant County: Dayville, *Henderson* 5505 (CA, DS, G, UO). Wheeler County: Fossil, *Henderson* 5503 (CA, DS, G). Crook County: Ochoco River, *Cusick* 1675 (DS, G, UC). Deschutes County: Bend, *Abrams* 9601 (DS, Po).

The range of *Penstemon richardsonii* is nearly confined to the east of the Cascade divide, while that of *P. diffusus* is mostly to the west of that summit. The two meet at such points as the gorge of the Columbia River. The gap in morphological characters between these species, however, is greater than their geographical differences. Differences in leaf-size, leaf-lobing, pubescence, glands and form of the inflorescence, calyx size and corolla size are those that might be anticipated between species respectively occupying relatively arid and moist habitats. The larger corolla and often exserted sterile filament of *P. richardsonii* are characters that further separate it from *P. diffusus,* but these are perhaps not directly attributable to climatic differences. Despite the width of their morphological separation, *Penstemon diffusus* is doubtless the living representative of the ancestral type that gave rise to *P. richardsonii.*

There is considerable variation within *P. richardsonii.* The majority of individuals collected have deeply cleft or parted leaves whose general outline is broadly lanceolate; but in northeastern Wash-

ington (Spokane County) the leaves are impressively narrower than this; and in north-central Oregon the leaves are elliptic and merely serrate or toothed. Differences as striking have been noticed in the habit, pubescence, corolla-size, beard of the sterile filament, etc. But the distribution of these variations is very imperfectly known and intermediates are frequent, so it has been impossible to classify any of them nomenclatorially.

18. **Penstemon triphyllus** Dougl.

Penstemon triphyllus Dougl. ex Lindl., Bot. Reg. 15:t. 1245, 1829.

Subshrub 2–8 dm. high: herbage sparsely to densely puberulent below inflorescence, the leaves sometimes entirely glabrous, the inflorescence glandular-pubescent: leaves 2, 3, or 4 at a node or even alternate, entire to coarsely dentate, but more often pinnately toothed or cleft, these remote teeth very short and sharp to narrowly elongated, if cleft the lobes often again toothed, linear to narrowly lanceolate in outline, 1.5–4.5 (rarely –7) cm. long, 1–8 (rarely –17) mm. wide; basal short-petiolate; upper cauline sessile: inflorescence an elongated panicle, simple to few-branched; peduncles usually divergent from main axis: calyx 4–5 (–8) mm. long; sepals narrowly lanceolate to elliptic or broadly ovate, entirely herbaceous, the margins entire: corolla blue-lilac, the throat striped within, 12–15 (–19) mm. long, usually glandular-pubescent without, usually glabrous within or with some pubescence on lower lip at orifice: lower pair of stamens reaching summit of throat or exserted, upper pair nearly as long, filaments usually glabrous, sometimes with short white pubescence near tip, the sterile one heavily yellow-bearded for outer ½ its length; anthers 0.9–1.3 mm. long: capsule 4.5–7 mm. long, barely exceeding the appressed sepals: seeds 0.75–1.2 mm. long.

Western Montana, eastern Idaho, western Idaho and adjacent Washington and Oregon.

Key to the Subspecies of Penstemon triphyllus

A. Leaves linear to narrowly lanceolate, usually ternate; inflorescence a mixed panicle; sterile filament heavily bearded.....18*a*. **typicus**

AA. Leaves lanceolate to narrowly elliptic, usually opposite; inflorescence more congested; sterile filament lightly bearded.....18*b*. **diphyllus**

18a. **Penstemon triphyllus** subsp. **typicus** nom. nov.

Penstemon triphyllus Dougl., l.c. Douglas's description is given at this reference; the remaining data being supplied by Lindley. I have a photograph of a Douglas specimen in Bentham's herbarium, in which the label reads: "On dry rocky places near the sources of the Wallawallah river in the Blue Mountains. 1826."

Plants 3–8 dm. high: leaves ternate, entire to cleft, 1.5–4.5 cm. long, 1–6 mm. wide: inflorescence a mixed panicle: sterile filament usually densely bearded all the way around for outer ½ its length.

Common along the basalt cliffs of the Snake River and its tributaries in western Idaho and adjacent Washington and Oregon, at elevations of 250–500 m. "According to Mr. Douglas, by whom this was detected, it is a common plant, on decomposed dry granite, or schist rocks, on the Blue Mountains of North-west America, in the district watered by the river Columbia; it is also found on the mountains to the southward in northern California." (Douglas often used the term "Upper California" for much of the region now included in eastern Oregon and southern Idaho.)

IDAHO. Nez Perces County: valley of Clearwater River, *Sandberg, MacDougal & Heller* 284 (CA, G, Po); near Lewiston, *Ferris & Duthie* 1302 (DS); mouth of Salmon River, *Eastwood* 13307 (CA). WASHINGTON. Whitman County: Wawawai, *Keck* 384 (Berlin, CA, CI, DS, G, Geneva, Kew, Miss, Phila, Po, UC); Riparia, *Keck* 389 (CI, DS, G, Po, UC). Klickitat County: Rockland, *Suksdorf* 998 (G, UC, according to Suksdorf, this plant was evidently brought down the Columbia River by flood waters). OREGON. Wallowa County: Imnaha River, *Cusick* 866 (G, UC); Snake River, *Cusick* 2220 (G, UC); Grande Ronde Canyon, *Applegate* 6465 (DS).

18b. **Penstemon triphyllus** subsp. **diphyllus** (Rydb.) comb. nov.

Penstemon diphyllus Rydb., Mem. N. Y. Bot. Gard. 1:349, 1900.

Plants 1.5–4 dm. high: leaves opposite, sinuately dentate or serrate, 2–8 cm. long, 5–17 mm. wide: inflorescence a more floriferous panicle than in *typicus;* sterile filament usually moderately bearded on upper side for outer third its length.

Frequent in the Rocky and Bitter Root Mountains of western Montana, and adjacent central Idaho, at elevations of 1000–1800 m. "Montana: Mullen Pass, 1860, *J. G. Cooper;* Soap Gulch, Silver Bow Co., 1888, *Tweedy,* 72."

MONTANA. Powell County: Deer Lodge Valley, Aug. 7, 1905, Aug. 16, 1905, *Jones* (Po). Deer Lodge County: Anaconda, *Albright* 1 and 3 (RM). Missoula County: Missoula, *Kirkwood* 1546 (UC). Granite County: Hell Gate Canyon, *Watson* 306 (G). Ravalli County: Darby, July 30, 1909, *Jones* (Po); Alta, July 22, 1909, *Jones* (Po). IDAHO. Lemhi County: Salmon, *Payson* 1751 (CA, G, RM).

Relationships of Penstemon triphyllus

This species is clearly related most closely to *P. richardsonii.* It represents a reduction from that species to a form better suited to exist on the very dry cliffs of the Snake River and tributaries where it abounds. Aside from the general reduction in size of the various parts, the most noticeable difference between the two is in corolla-shape. In *triphyllus,* the corolla is funnelform, with tube as long as the throat, and limb expanded with rotate lobes; which is in contrast to that of *richardsonii* in which the tube is short, the throat ventricose, and the limb better defined into an upper and lower lip. The usual occurrence of three or four leaves at a node is a striking characteristic of *triphyllus.*

The subspecies *diphyllus* is a more luxuriant form in keeping with its less xerophytic habitat. The difference between these subspecies consists mainly in the relative leaf-width. Seedlings and vegetative shoots from injured plants of *typicus,* collected in September, on the Snake River in Washington, bore leaves as large or larger than any seen thus far of *diphyllus,* while the normal plants at this station bore leaves that were almost linear. Opposite leaves occur at time on *typicus;* so no character has been discovered that would warrant the retention of *diphyllus* as a species.

19. **Penstemon glandulosus** Dougl.

Penstemon glandulosus Dougl. ex Lindl., Bot. Reg. 15:t. 1262, 1829. Douglas' description is given at this reference; the remaining data being supplied by Lindley. I have a photograph and notes, furnished by Hall, of a specimen in the Hooker herbarium that was undoubtedly collected by Douglas. Its label reads: "On the undulating ground of Lewis and Clark's river, near the Forks . . . ." Hall reports a duplicate in the Bentham herbarium.

Penstemon staticifolius Lindl., Bot. Reg. 21:t. 1770, 1836. "Sent to the Horticultural Society by the late Mr. Douglas from California." (Douglas often labeled material from eastern Oregon and southern Idaho as from "Upper California.")

Perennial herb 5–10 dm. high: herbage glandular-pubescent throughout with very short downy hairs tipped with minute glands, more viscid within inflorescence, the leaves often only puberulent: leaves dimorphous; basal with blade lanceolate to elliptic, the petiole ½ as long, usually entire, 4–30 or 40 cm. long (including petiole), 15–60 or 75 mm. wide; upper cauline lance-ovate to cordate, amplexicaul, almost connate-perfoliate, sharply serrulate or serrate, 4.5–9 cm. long, 20–40 mm. wide: inflorescence an interrupted spike of 3–5 (–7)

distinct verticillasters or sometimes the peduncles elongate to form a narrow thyrsus: calyx 10–15 mm. long; sepals lanceolate, entirely herbaceous, the margins entire: corolla pale lilac to light violet, 28–45 mm. long, glandular-pubescent without, glabrous within or with few long hairs on lower lip near orifice: lower pair of stamens reaching well into lip, upper pair 5–10 mm. shorter, retained within throat; filaments glabrous including the sterile one (or the latter rarely with few hairs at tip); anthers 2.0–2.25 mm. long: capsule 10–14 mm. long, exceeded by the appressed sepals: seeds 2.0–3.25 mm. long.

Uncommon at isolated stations in western Idaho, southern Washington, and northern and northeastern Oregon, at elevations of 200–2000 m. "In the dry, gravelly, or rocky channels of mountain torrents in the Rocky Mountains, lat. 47° north, and at the base of the Blue Mountains on the banks of the Kooskooskee river, 6300 feet above the level of the sea, it occurs frequently.—Douglas."

IDAHO. Nez Perces County: June 1892, *Sandberg* (DS); Lewiston, *Heller* 3128 (UC), May 20, 1894, *Henderson* (RM); Hatwai Creek, *Sandberg, MacDougal & Heller* 169 (CA, DS, G, Po). Canyon County: Big Willow, *Macbride* 139 (DS, G, RM, UC). WASHINGTON. Klickitat County: mountain tops, Columbia River, June 6, Aug. 1881, *Suksdorf* (CA, UC); Klickitat Hills, *Howell* 1517 (UC). OREGON. Wallowa County: Snake River, *Cusick* 1893 (Po, RM, (UC); Imnaha, *Sherwood* 137 (DS). Baker County (?): Eagle Valley and vicinity, *Cusick* (UO). Wasco County: 10 miles S.E. of The Dalles, *Thompson* 4176 (DS). Hood River County: Mount Hood, May 1886, *Davidson* (Po).

Penstemon glandulosus does not grow in the rock-clefts commonly sought by the four preceding species, but rather chooses the open hillsides where soil is more abundantly available.

This plant does not appear to be as closely related to any of the preceding four species as they are to each other. Indeed, it seems to be an isolated species of considerable age. The comparatively wide distribution into small isolated colonies would support the view that *glandulosus* is no longer a progressive form. The general habit, and the form of the leaves and inflorescence point to an origin of the same source as that of *P. diffusus*.

Penstemon pickettii St. John, Proc. Biol. Soc. Wash. 44:33, 1931, is a doubtful species. *Type.*—"Washington: rock slides, Ribbon Cliff, Columbia River north of Wenatchee, Chelan Co., collected July 16, 1928, flowered in garden in Pullman, July 18, 1929, *F. L. Pickett* 1390 (type in Herb. State College of Washington); fruiting specimens on Aug. 10th and 19th, 1929." Neither the type nor other specimens of this have been accessible from the Herbarium of the State College of Washington as yet. Material has been sent out as this, from a garden plant brought from the type locality at the same time as the type, which, however, was

genuine *P. richardsonii*. The original description points out no specific character that could be used to separate this from *P. richardsonii* unless it is the "white glandular pilose" covering of parts in the inflorescence; but comparison of specimens of the two species must decide whether this feature is more than a misinterpretation of terms. Unfortunately, the author of *P. pickettii* failed to contrast his species with *P. richardsonii*, with which it grows and which is undoubtedly its closest known relative. Pennell considers this a good species, having seen a garden plant of it of which he writes me, "it was a plant with decidedly inflated corolla and showed remarkably short corolla-lobes." On the strength of such characters it may eventually be retained by authors in a subcategory under *P. richardsonii*.

Carnegie Institution of Washington
Division of Plant Biology,
Stanford University, California.

INDEX

PAGE

Azurei 376
Bridgesiani 375
Glandulosi 376
Heterophylli 376
Penstemon *amoenus* 418
argutus 415
azureus 401, 402
var. *ambiguus* 386
subsp. angustissimus 402
var. *angustissimus* 402
var. *jeffreyanus* 403
subsp. parvulus 406
var. *parvulus* 406
subsp. typicus 402
bridgesii 375
var. *amplexicaulis* 376
rostriflorus 376
caesius 378
cinerascens 390
cusickii 381
diffusus 415
dimorphus 392
diphyllus 422
glandulosus 423
glaucifolius 402
gracilentus 377
var. *ursorum* 390
heterophyllus 408, 411
subsp. australis 411
var. *australis* 411
var. *azureus* 403, 409
var. *latifolius* 385
subsp. purdyi 409
subsp. spinulosus 410
subsp. typicus 411
jeffreyanus 403
var. *parvulus* 406

PAGE

kingii 387
laetus 389, 392
subsp. filiformis 394
subsp. leptosepalus 393
var. *leptosepalus* 393
subsp. roezlii 390
var. *roezlii* 390
subsp. sagittatus 395
subsp. typicus 392
latifolius 385
leonardii 383
leucanthus 411
macbridei 381
neotericus 398
parvulus 406
pickettii 424
platyphyllus 385
purpusii 414
richardsonii 419
rivularis 419
roezlii 390
var. *violaceus* 387
rostriflorus 375
scapoides 379
sepalulus 386
scrrulatus 415
spinulosus 410
staticifolius 423
suffruticosus 418
tenellus 402
triphyllus 421, 422
subsp. diphyllus 422
subsp. typicus 422
venustus 418
violaceus 387

SAMUEL BONSALL PARISH

BY

WILLIS LINN JEPSON

University of California Publications in Botany
Volume 16, No. 12, pp. 427–444, plate 32
Issued February 27, 1932

University of California Press
Berkeley, California

Cambridge University Press
London, England



Plate 32

S. B. Parish

SAMUEL BONSALL PARISH

BY

WILLIS LINN JEPSON

In the early summer of 1872 S. B. Parish settled on a farm near the town of San Bernardino in the coastal region of Southern California. He had come somewhat recently from the eastward of the Rocky Mountains, within a relatively short time from the far eastern United States, and the native vegetation, so utterly unlike anything he had ever known before, attracted his interest in days of leisure. This interest grew with the years, and as it grew he extended the range of his holiday journeys in the field until it comprehended all of southern California, a term which, it is well to note, has a topographic rather than a strictly geographic significance and comprehends the eight counties lying south of the Tehachapi Mountains.

Samuel Bonsall Parish had no special training in botany but it was often said in that day, and is still said by some, that if a boy were really alive, and had fine native capacities and a sound course in the five or six fundamental subjects constituting a college education, he could do any one thing in life that he chose. That thesis is supported by a thousand illustrations and Mr. Parish proved to be one of them. Born in Paterson, New Jersey, January 13, 1838, the son of Daniel Parish, a Methodist minister, and his wife, Eliza Gray Bonsall, he entered Wesleyan University at Middletown, Connecticut, in the fall of 1854 and at the end of his sophomore year transferred to New York University in New York City where he was graduated with the degree of Bachelor of Arts in the class of 1858. In college he studied Greek, Latin, mathematics, physics, and chemistry. Languages were agreeable to him, but for chemistry he had an especial taste. Though he found no difficulty in mathematics, he disliked the subject and when the senior year came he exercised an option between calculus and Hebrew, and chose Hebrew, which he found very easy. Following his graduation he taught in a private academy at Ottawa, Illinois, for a year, and then in the Barton Academy at Mobile, Alabama, until the breaking out of the Civil War in 1861, when he returned to New Jersey. Later in the same year he went to Kansas, enlisted in Company K, Second Kansas Volunteer Cavalry, in which he served during

the war, taking part in several considerable and many minor engagements, and was mustered out as First Sergeant in April, 1865. He was now joined by his brother, William Fletcher Parish, who had served during the war in a New Jersey infantry regiment, and the two started off into the west together, prospecting and mining in various parts of Colorado, Utah, Arizona, and California. In 1872, the two brothers bought a ranch in the San Bernardino Valley near the old town of San Bernardino, and engaged in fruit growing and other agricultural operations. Here in this valley the available labor supply consisted of Mexicans who spoke only the Spanish language. In the East Mr. Parish had studied Spanish, but seeing the need for greater proficiency he sent home for his Ollendorf book, the text in vogue in that day, and mastered Spanish in such wise that he was enabled to converse fluently with the Mexican rancheros.

Although there was a little botany in the college courses at Wesleyan and New York, the work was poorly presented and he derived small profit from it. He may thus be said to have had practically no school training in the science that afterwards dominated his interest. Yet he manifested quite early a natural predilection for the study of plants, since he made small collections of the more showy flowers while in Illinois, Alabama, and Colorado. At San Bernardino he was without books at the beginning, save for one or two nurserymen's catalogues and, indeed, a botanical library was accumulated only very slowly and after many years. At that time there were no botanists resident in southern California and he was thus extremely isolated. It fell out, however, that J. G. Lemmon, on a visit to San Bernardino, was brought to the Parish ranch by W. G. Wright, the amateur entomologist of that town. The temperamental oddities of Lemmon made a very unfavorable impression upon Mr. Parish, but later through Wright he met Dr. C. C. Parry, formerly botanist of the Mexican Boundary Survey, and his delight, in consequence, was very great. Gifted with a genial and engaging personality, long a student of western botany, Dr. Parry gave freely and generously to every one of his store of botanical knowledge. About three miles east of Redlands one Craft had started a hotel at Crafton. It was the place for tourists at that time and Dr. and Mrs. Parry made it their residence for several months or more; a year or so later they wintered in San Bernardino and so became more immediate neighbors of the Parishes. In company these two men, Dr. Parry and Mr. Parish, went on field excursions and as a result of their friendship Dr. Parry

brought Mr. Parish into correspondence with Asa Gray, resulting in a life-long and mutually beneficial interchange of ideas, facts, and specimens with the Harvard botanist.

Set down in the midst of varied and abundant floral wealth, Mr. Parish was well situated with reference to that which he had to do. Rising abruptly from the floor of the San Bernardino Valley, only a few miles away and in full view from the dooryard of the Parish home, the range of the San Bernardino Mountains culminates in Mt. San Gorgonio as its highest point, 11,485 feet. The highly distinctive chaparral region of these mountain slopes is bounded above by a coniferous forest belt studded here and there with flowering meadows and bordered below with the open grasslands of the low hills and valley floors. This area, the whole of it, provided right at hand a new, accessible, and unique territory as yet unsurveyed by any botanist. Nearly every trip into the field turned up new species and increased the glamour of exploration. As the years passed his curiosity ever grew as to the composition of the southern California vegetation as a whole and each spring or fall, during the slack times on the ranch, he ranged farther and farther afield. For his expeditions a strong wagon was specially built with reference to the difficult and rocky mountain terrain or the lonely and sandy deserts. A low-hung body and broad tires on the wheels made it suitable for carrying a heavy load of hay, barley, and water, as well as the food supply and camp outfit. Westward he explored the sea beaches of the Pacific Ocean, eastward the San Jacinto Range, southward the complex of mountain ridges and web of hills that make San Diego County until one reaches the Mexican border. Very early in these years he made his way through the passes in the ranges that separate coastal southern California from the deserts—through the Cajon Pass into the Mohave Desert, through San Gorgonio Pass into the Colorado Desert, through Morongo Pass into the region of Warner's Well. One of these expeditions into the desert, that of 1915, carried him as far as Death Valley; and in other years he explored the eastern Mohave.

Life on a pioneer California ranch was hard and difficult, but Mr. Parish possessed a fine physique and endured continuous labor well. After the evening meal he rested or slept in his chair for ten minutes, after which it was his custom, unless there were guests, to go to his room and study the plants of his collections. At 9 o'clock he retired, in a few minutes was asleep, and rose the next morning refreshed for another day's work in the fields. He was never ill.

His first printed paper appears to be of the year 1888, published sixteen years after he first began to make observations on the native plant life in California. From that time onward, until 1926, he published in botanical journals and in bulletins and proceedings of learned societies something like one hundred papers, most of them rather brief but all representing some distinctive contribution to the knowledge of the flora of southern California. His work was done carefully, methodically, and deliberately, with the result that his papers as a whole are remarkably even in quality—they strike a high level. Going afield in days of vacation from the ranch, collecting, recording, and bringing home his plants for study, observing judiciously and widely, it was thus that he grew in knowledge of the botany of his region. It is this knowledge, painstakingly acquired and patiently seasoned, which goes into his papers—but each paper is restricted in scope so that it might be finished within the limits of the brief moments of freedom from ranch responsibilities. Careful, clear-sighted, sagacious, he went steadily on, doing this thing which pleased him so well, an unhurried kind of work endowed with lasting satisfactions. A concise summary of a portion of his field work may be found in his essay, "A Sketch of the Flora of Southern California" (Bot. Gaz., 36:203–222, 1903). Another paper sums up his botanizings in the mountain range nearest his home. It is entitled, "An Enumeration of the Pteridophytes and Spermatophytes of the San Bernardino Mountains, California" (Plant World, 20:163–259, 1917). It contains a commentary followed by an annotated list, a paper much used by botanists, and recalling in usefulness his earlier paper on the "Distribution of Southern California Trees" (Zoe, 4:332–353, 1894). Such revisions and monographic treatments as "A Group of Western American Solanums" (Proc. Cal. Acad., ser. 3, Bot., 2:159–172, 1901), "A Contribution towards a Knowledge of the Genus Washingtonia" (Bot. Gaz., 44:408–434, 1907) and "The Californian Paroselas" (Bot. Gaz., 55:300–313, 1913) are authoritative. In addition there were careful papers upon teratological, ecological, and distributional topics and reviews of new publications. He gave much thought to immigrant plants and published concerning them. In 1913 he contributed "A Catalogue of Plants Collected in the Salton Sink" to the monograph on the Salton Sea issued by the Carnegie Institution of Washington (Publ. 193).

The papers of Mr. Parish have a further value which may fittingly be emphasized. All of them rest upon, are validated by specimens

carefully labeled and recorded. From the beginning he appreciated well the importance of such validating records and consequently his herbarium steadily grew into a large collection and became highly important on account of the explicit statement of collection facts associated with each specimen and because it formed the most essential and valuable foundational record of his various subjects of research.

The temperament of Samuel Parish was singularly even. Without question he must have been on occasion stirred by indignation or by deep annoyance, but he maintained a remarkable control of his emotions and only once in his long life was he known to give way to anger. Genial in disposition, thoughtful and considerate of others, highly amiable in his relations, he envied no man and serenely looked for the best in human nature. With all this, he yet had strong determination and resolution in his make-up, the capacity to exhibit firmness when firmness was needed, to assert when necessary the substantial underlying dignity of his character.

About 1890 the militant crusade in the United States for the reformation of plant nomenclature began to gain headway and drew into the movement a large number of prominent American botanists. An incident connected therewith illustrates well the character of the San Bernardino botanist. He had sent to E. L. Greene, then Professor of Botany in the University of California, a paper for publication. Recognizing Professor Greene as the real leader in nomenclatorial reform, he had amiably used in his paper certain names merely because he felt that Professor Greene preferred them. The letters of Professor Greene attempted to persuade his correspondent to a complete separation from the old way. The letters of Mr. Parish in reply show so well the firm groundwork of his character that they are here given in full. Professor Greene, as is well known, possessed mastery of the art of clear, convincing, and vigorous communications. It were only simple justice, then, to print alongside of the Parish letters the letters of Professor Greene, since we may be sure that his side of the case was written in persuasive, lucid, and forceful terms. Unfortunately his correspondence with Mr. Parish was lost in the Berkeley fire of 1923. The disaster which occasioned the necessity for this explanation must, in this case, be specially regretted. The correspondence in question was, however, an amiable one, as between good friends, and thus one may venture to print only one side of it, since no better way can be found to illustrate so happily certain phases of Samuel Parish's character.

San Bernardino, Cal.,
24 Mch., 1895.

My dear Prof. Greene:

It seems to me that all the time and learning that have of late been so lavishly bestowed on studies of nomenclature produce a very inadequate return. However interesting they may be historically they do not advance our knowledge of things in the least. If one discovers that a spade was first called by some other name it does not assist us in understanding the nature of a spade.

Names seem to me mere tools, handles by which we get hold of things—the most convenient and certain are the best. Considerations of sentiment should have no influence, and still less do they come within the domain of morality. Whoever adopts the Linnean era accedes to this proposition.

Rules which lead to changes may be proposed by anyone, but they are mere individualisms or provincialisms until they are adopted by representatives not of a single country, but of the whole botanical world. The only reason for accepting the Rochester code would be that they would result in a certain and a permanent nomenclature. It does not appear that either will result from them; in the hands of different experts they produce discordant conclusions, and their provisions will produce more synonymy and less stability than the old system with all its faults. I think you have yourself distinctly asserted that they are merely temporary, and must at last be replaced by others that shall not ignore the Prelinneans.

For these reasons I have not been able to share the enthusiasm for the new rules that animates most of our American botanists, so that I continue to think of plants under their old names, and when in my isolation I sometimes have occasion to speak of them I do it by the old names, and I would use them if I were to print anything myself. But as it is not a matter of conscience with me I would not if in the company of reformed botanists, who were all using the new names, make myself conspicuous by refusing to use their nomenclature. So, in offering a contribution to your journal I thought it would be more acceptable if I complied with the nomenclature of that journal. Indeed I had got the impression that this was expected of contributors, having been informed by one that his paper had been editorially emended in this respect. So I meant to use the latest names, and so wrote *Juncoides,* and had written *Plantagenella,* but before making a fair copy the new List came and gave us back *Limosella* as the very latest. I would have written *Ptiloria* but really the name had slipped my memory. I know it was careless, but with the monthly flood of changes that is poured upon us it is not altogether inexcusable.

Now I fear I have taken too much of your time over a matter really of little importance, but it seems impossible to get on the subject of nomenclature without being somewhat wordy.

We are having lovely weather, and the country is charming in the luxuriance of its young vegetation. Plants are getting advanced enough to allow one to begin to collect. I was out yesterday, and saw lots of your beautiful *Lathyrus laetiflorus,* the common species here.

Faithfully yours,

Sam. B. Parish.

San Bernardino, Cal.,
2 April, 1895.

My dear Professor Greene:

I feel really disappointed that after I had laid aside my own preference in nomenclature in order to fit my little paper for admission to your journal, I should, after all, have failed. However, I shall let it be a lesson to me, and as this is the first time that I have ventured into the bogs of reform, so it shall be

the last, and not even considerations of friendship shall tempt me from a conservative footing hereafter. It is wrong even to comply at all with what one does not really believe in.

Are you not a little hasty in saying that "all men except Adanson (1793) and Coville (1895) have approved the rejection of adjective names like Juncoides"? If you will turn to the new Botanical Club List[1] you will find not only that name, but Elatinoides, Ilicioides, Capnoides, and, I think, one or two more like them. Now this list is the work of a Board of Editors[2] which embraces some of the leading botanists of America; as none have repudiated any part of it, it is fair to say that they stand responsible for it. It is the fair, consummate flower of the reform rules which eliminate the personal equation and lead to an infallible and certain nomenclature. In the opinion of the Torrey Bulletin it has the approval of over three-fourths of the working botanists of America and no work of magnitude can hope for future success which does not conform to it. Yet you tell me that some of the names there established are admitted only by Coville among the present generation. If this is the certainty and unanimity that the new rules are to give us what profit have we from them?

Politicians and even theologians have come to see that a differing view of a question does not involve any moral turpitude. A couple of hundred years ago they used to call each other "thieves and pirates," but it is hardly worth while at this day for botanists to pick up these antiquated and discredited weapons. So much, you know, depends upon the point of view. Perhaps this is the core in our own disagreement. If I thought with you that an author retained a proprietary interest in a plant that he was first to name, I would be quite as unwilling as you are to deprive him of it. When an author happens on a plant which he thinks new, he proposes a name for it, not for his own glory—I know ill-natured people intimate that this is not always true, but usually it is—but for the advancement of knowledge. If his fellows agree with him and accept it they do not add his name to it to glorify him, or to give him "credit," or because it is in any way a matter of right that it should be there, but simply to make it certain that it is the plant that Smith described under that name, and not the one Jones may perhaps have given the same name to. If we could have certainty without cumbering ourselves with authors' names it would be folly to add them. In the same way we use the first proposed name to avoid confusion and uncertainty, and all questions of "credit" or right are foreign to the matter. If we could have greater certainty and greater advancement of knowledge by using the second or the last proposed name it would be folly not to use them. The end of science is the advancement of knowledge, not the glorification of individuals. The place to give an author credit or to right the wrongs of suppressed ones is in their biographies or in botanical history. While they are living their own works generally give them greater reputations than posterity is willing to indorse.

Holding as you do that there is a sort of divine right in priority I have admired you for having the courage of your opinions. If it is a matter of right and not of convenience, the man who wrote before 1753 has as much claim to justice as those who have come after. No date can stop right, and you do well

---

[1] List of Pteridophyta and Spermatophyta growing without cultivation in northeastern North America. Prepared by a committee of the Botanical Club, American Association for the Advancement of Science. (Memoirs of the Torrey Botanical Club, 5:1–377. 1893–1894.)—W. L. J.

[2] N. L. Britton, John M. Coulter, Henry H. Rusby, William A. Kellerman, Frederick V. Coville, Edward L. Greene, William Trelease, Lucien M. Underwood, Lester F. Ward.—W. L. J.

to insist on going back as far as you can for what is really the first name. Of course the application of this principle will overturn not merely the old but also this new nomenclature. To me this is a reductio ad absurdum, for it makes the means of more importance than the end; but I see no escape from it if we admit that priority is to be respected as a matter of right and not of convenience.

I am aware that you have reinstated a number of prelinnean names, and I realize that it is a work of time and difficulty to find in all cases the original name, and that till this is done later names must be retained, but am I to understand that it is your purpose to go on and whenever you ascertain the priority of a prelinnean name to restore it? Consistency would seem to require it. And holding these opinions are you consistent in giving editorial endorsement to the Bontanical Club List which is guilty of "piracies and robberies" on the property of the unfortunates who preceded Linnaeus, and in giving your adherence to the Rochester code which authorizes them?

And why, why do you gird at our friends in the East for their youth; for my own part it is the one great thing which I envy them, and for which I would gladly exchange some of my matured experience.

Faithfully yours, Sam. B. Parish.

San Bernardino, Cal.,
April 7, 1895

My dear Professor Greene:

It is much pleasanter to find agreements than differences with one's friends, so that I am glad to find that we are at one, although arriving by different roads, in repudiating the Rochester Code, and its pattern exhibit, the New Plant List.[3] As to the stability to be hoped for from them I was somewhat amused in looking over Britton's Report on Arizona Plants,[4] just at hand, that Coville's *Larrea tridentata* comes back to *L. Mexicana*, and that Scribner who on Jan. 3, '94, in the New List put the species of Setaria under Chamaeraphis, on the 22d Oct. last in the Arizona Plants restores them to Setaria, but on Dec. 16 forgets to note his change of heart in the Appendix to the New List, where the latest thoughts of the editors should have found record. I am too old to follow such agility, and am confirmed in my resolution of abiding on conservative grounds till this storm be overpast.

I am not a little puzzled to understand how you as one of the botanical leaders in America can reconcile your private condemnation of this New List with your public position as a sponsor for it. As a member of the Editorial Board I think you may be justly held responsible for it, so long as your disclaimers are made only privately to your friends and not to the botanical public. And while I knew you did not consider that the Rochester code went far enough, I certainly thought it had your general approval. I am glad to learn from you that it really was adopted under the influences and pressure you describe, and without the intelligent purpose of most who voted for it. I had suspected this, but of course could not *know* it. Its success shows how much can be done by "push" and industry.

---

[3] See footnote 1.

[4] N. L. Britton and T. H. Kearney, Jr. An enumeration of the plants collected by Dr. Timothy E. Willcox, U. S. A., and others in southeastern Arizona during the years 1892–94 (Transactions of the New York Academy of Sciences, 4:21–44. 1895). Professor Scribner's unlucky note on Setaria and Chamaeraphis occcurs on page 24.—W. L. J.

Now just one word more on the *-oides* names. With my ideas of convenience I am perfectly ready to change them; but how can you do it with your rigid ideas of right? Is the pirate to plume himself on his virtue if he only robs the few ships who have an outlandish jibboom? If you may rob Adanson of his adjective names because they offend your sense of propriety why may not I deprive Hoffmann of his detestible Razoumoffskia, or Rafinesque of some of the barbarisms with which he offends me? The whole thing must stand or fall together.

You are the nearest to a conscience-botanist of any, but it seems to me you are a little oblique on the *-oides* question. But conscience in nomenclature is a curious thing. Coville[5] wrote to me very seriously on the immorality of omitting that *i* in Juncoides, as MacMillan[6] had done. MacMillan's tender conscience would not permit him to correct the spelling of Scoria. Britton[7] is more hardened, and does not hesitate to change the spelling and even the forms of names to suit his ideas of fitness. But with me the only point of morals in nomenclature is that no one should be represented as the author of a name which he really published under a different form. If you today published a Bikukulla the supposition would be that you preferred that form, and Dr. Britton would have no right to add your name to a different form, for it would be untrue; he would himself be the author of the new form, not you. The same rule should apply to the dead, who cannot rise up and protest. Of course it is right enough to correct obvious typographical errors.

You are right as to persons like myself who love a science, but have little time at their disposal, and few books and limited collections to aid them. In many—in most things they must follow authorities. If a name of Rafinesque is proposed to take the place of one now in use they have not the book to turn to and satisfy themselves that the description is sufficiently accurate to compel the change. If a new species is proposed to be set off from an old one they have not the suites of specimens to examine and convince themselves of its validity. They must follow authority. The conservative will incline to those who seem the least willing to make changes, and to where they have been accustomed to look for guidance, from where they have derived their ideas of specific and generic limitations. The radical will follow those they regard as progressive, and who are always finding something new, and the young, again, will be disciples of their master. Our limitations inevitably produce some inconsistencies for we do not wish to be absolutely blind followers of any one, and even our masters, with all their advantages, are not entirely exempt from inconsistencies. But I will promise you not to be again deliberately inconsistent, and to adhere, to the best of my knowledge, to what my judgment approves and to keep my skirt clean from the reform nomenclature.

Faithfully yours,

SAM. B. PARISH.

---

[5] Frederick Vernon Coville, Botanist, Bureau of Plant Industry, United States Department of Agriculture.—W. L. J.

[6] Conway MacMillan, Professor of Botany, University of Minnesota, author of "The Metaspermae of the Minnesota Valley," 1892, a somewhat ponderous work (heavily weighted with a multitude of bionomials), which put into practice the principles of the reformed nomenclature (Rochester code). It was widely hailed by the reformers as one of the signs of a new day.—W. L. J.

[7] Nathaniel Lord Britton, Professor of Botany, Columbia College, New York City.—W. L. J.

Mr. Parish kept well to his promise, paid scant attention to nomenclature as a subject by itself, and devoted his powers to inquiries regarding the distribution, relationships, and life histories of the native plants that grew about him. So it is that his name has for a longer period been associated with the natural history of the southern California vegetation than that of any other botanist and his work is memorialized by many a species of the mountains and mesas, of the hidden valleys and desert washes, which have been named in his honor. A peculiar endemic genus of the Mohave Desert, where he did some of his best work, was named in commemoration of him by Asa Gray. In proposing the new genus Asa Gray writes him from Cambridge, on June 20, 1882, saying:

> But my eye caught one thing, which I knew would repay examination. And to-day I have taken it up. It is one of your smallest plants, no. 1328, but most interesting,—being a second genus of the small and rare group to which Nemacladus belongs. I rejoice at the opportunity of naming the genus in your honor—one of your own discovery. But it is a *wee* plant. And perhaps you would prefer to wait till you turn up something which can be cultivated and become common or ornamental. If so, you must let me know. Otherwise I shall fix this little plant as the Parishella Californica.
>
> I must take the generic name in that form, as Sir Jos. Hooker has several years ago published a Parishia from the East Indies, in a very different order.
>
> But, though this is not a showy plant it is a *most interesting* find, a most distinct little genus. If you will have it, well. If not I can easily make a characteristic name for it. I like to call it Californica, if it takes your name, because I wish to have your name for ever connected with California—the botany of which you have done so much for.

During a period of forty-eight years, the Parish home in the San Bernardino Valley was much visited by botanists. As time ran on scores and scores of botanists wished to see and talk with the man who knew his region so well and whose personality was so pleasing. In the very early day came Edward Palmer, Edward Lee Greene, C. G. Pringle, and George Engelmann. Accompanied by Mrs. Gray, Asa Gray, seeking health, visited the Parishes in 1885, and we find Mrs. Gray writing from Santa Barbara: "We have such pleasant recollections of our visit to you! And I think of those beautiful mountains—Dr. Gray seemed really to take such a decided turn for the better in the quiet and comfort of your house." In later days there was C. S. Sargent, M. S. Bebb, Volney Spaulding, Hugo de Vries, Ellsworth Huntington, J. N. Rose, and others too numerous to mention, but all had a welcome, genuine and felicitous.

On October 3, 1883, Mr. Parish was married to Mary Eliza Bonsall at Newark, New Jersey. She was an educated woman who proved a delightful and happy helpmeet. Without interest in botanical science she yet sympathized completely with all his plans and projects and often accompanied him on his botanical expeditions. In 1917 the Parish Herbarium was sold to Stanford University and in 1920 the library to Pomona College at Claremont, California. On account of the advantages for Mr. Parish of the herbarium and library at the University of California, they removed to Berkeley in 1920. Soon after taking up his new residence Mr. Parish was appointed Honorary Curator in the University of California Herbarium and a little later Lecturer in Botany at Stanford University. The fire in Berkeley on September 17, 1923, consumed not only his residence but all its contents, including his books and unpublished manuscripts. He met this blow with a serene fortitude which was characteristic of his nature. The last field trip, a journey to the Mexican border near Campo, was made when he was eighty-one years of age. He passed away at Berkeley on June 5, 1928, in his ninety-first year.

The personality of Samuel Parish was singularly attractive. Simple in manner, natural and unaffected in bearing and in speech, both generous and modest, he was yet a man of quiet force with sober and reasoned convictions. With regular features and blue eyes, he had a kindly countenance which some of his friends thought characteristically British. In any event he was often mistaken for an Englishman. He was a member of Phi Beta Kappa, the American Association for the Advancement of Science, the California Botanical Society, and the Botanical Society of America. For this latter society the present writer was called upon to prepare a brief biography and he cannot do better than to repeat the closing words of that memorial: "It may truly be said that Samuel Parish was much beloved. His happy wit, his irresistible good humor and sound sense, his appreciative sympathy with common joys and sorrows engaged deeply the affections of all botanists who knew him. In him and for him Californians have only prideful and happy memories."

BIBLIOGRAPHY

Parry, C. C.
1881. A botanical establishment in southern California. Pac. Rur. Press, 21: 402.

Annual Dinner of the California Botanical Society. Personal reminiscences by S. B. Parish; portrait. Madroño, 1:71–75. 1922.

Jepson, W. L.
1929*a*. Samuel Bonsall Parish. Sci., 69:63. Jan. 18.
1929*b*. Samuel Bonsall Parish. Bot. Soc. Am., Publication 99:26–28. Botanical letters of other days, pp. 246–262 (MS).

Abrams, L. R.
1929. Memorial response at the California Botanical Society dinner. Madroño, 1:270–271.

BOTANICAL JOURNEYS OF SAMUEL BONSALL PARISH

1882–1919

For the following itinerary we are indebted to Mrs. Parish. A few notes and additions have been made by the writer. The Parish plant collections were distributed so widely that a complete itinerary would, on account of its permanent usefulness, be desirable, but the full records of the field trips were lost in the Berkeley fire.

1877–1880. Trips in the San Bernardino Valley. Later trips with Dr. Parry; often just for a day: once to Thousand Palms and other places on the Colorado Desert as far as Yuma; and at least once farther into Arizona.

1880–1881. Worked under C. S. Sargent for the United States Census, collecting specimens of trunks of trees. Later he collected the same kind of specimens for the Jessup Collection. While collecting for these objects he made trips into the mountains and deserts with George Vasey, Jr., C. S. Sargent, Geo. Engelmann, and C. G. Pringle.

1897, June. Riverside and San Diego counties, stopping at Warm Springs, camped one week on Palomar Mountain in Doane's Meadow, a beautiful park-like place with fine yellow pines and a stream lined with azaleas just going out of bloom; thence to the Cuyamaca Mountains, then across to the ocean at Sorrento, up the coast to Oceanside; return by way of Fairview and Riverside.

1901, May, ten days. Big Bear Valley by way of the Mohave Desert; return by way of City Creek road. On this trip accompanied by L. A. Greata. June, three days. Mill Creek Cañon.

1902–1906. San Bernardino Valley and foothills.

1907, March, ten days. Palm Springs of Mount San Jacinto. On this trip accompanied by W. G. Wright, of San Bernardino. April, latter part, Palm Springs of Mount San Jacinto.

1908–1911. San Bernardino Valley.

1912, June. Began work for Carnegie Institution as Associate of Desert Laboratory, Tucson, Arizona. July, October. Mecca and vicinity.

1913, spring. Colorado Desert. May 19–21. Mill Creek Cañon, San Bernardino Mountains. On this trip accompanied by W. L. Jepson. September. Mecca Phytogeographical Expedition. October. San Diego and the Colorado Desert.

1914, May, three weeks. Tecate Mountain, San Diego County. On this trip accompanied by Frank Stephens, of San Diego.

1915, Spring. Mohave Desert, on behalf of Desert Laboratory.

1916, April. Near San Bernardino; Los Angeles; Santa Catalina; Colorado Desert in San Diego County, collecting specimens of trees on behalf of C. S. Sargent of the Arnold Arboretum.—Coronado Islands, one day.

1882, April. Agua Caliente (Palm Springs, east base of Mount San Jacinto).

1884, July. Little Bear Valley, San Bernardino Mountains.

1885, April, four days. Lytle Creek Cañon and falls.

1886, June, two to three weeks. Big Bear Valley by way of Hesperia, Rabbit Springs, and Cushenberry Springs; return by way of Gold Hill and Holcombe Valley to Cox's Ranch, thence through the Cajon Pass.

1887, June. Fort Tejon by way of Cajon Pass and the San Bernardino Mountains; return by way of Elizabeth Lake and Los Angeles. Looking for Dalea arborescens for C. S. Sargent.

1888–1890. Many short drives of a day through San Bernardino Valley and foothills. Collecting for extensive exchanges.

1891, spring. Collection made of nearly a thousand specimens for George Vasey, United States National Herbarium. November, five days. To Fallbrook, in order to secure logs of *Quercus elegantula* and *Quercus macdonaldii* for C. S. Sargent (Jessup Collection).

1892, June. Big Bear Valley, San Bernardino Mountains, by way of the Mohave Desert; return over new mountain road to Little Bear Valley, along the range to Devil Cañon, down almost abandoned Devil Cañon road to San Bernardino. July 2–5. Mill Creek Cañon. Explored Snow Cañon.

1894, June. Big Bear Valley, San Bernardino Mountains, by way of Mission Creek, Warren's Well, Byrne's Cañon, and Rose Mine, to the valley; one day spent in Bluff Lake; return by mountain road, across the high country ("Rim of the World") to Waterman Cañon.

1895, June, few days. San Bernardino Mountains, Big Bear Valley. Ten days, Bluff Lake. Three days, Palmer Ranch.

1896, April 4–13. Palm Springs of Mount San Jacinto (Agua Caliente). May(?), Mohave Desert, Death Valley expedition, S. B. Parish and Ellsworth Huntington. September. Santa Barbara, Ventura.

1917, spring, one-day trips. Also Playa del Rey; Redondo; and Mohave Desert. One week. Bear Valley, by way of Mohave Desert, accompanied by Harley P. Chandler.

1918, May, two days. Big Bear Valley, by way of the Mohave Desert, return by Mill Creek road; accompanied by W. S. Cooper.

1919, June, five days. Colorado Desert beyond Campo for specimens of a tree for C. S. Sargent.

1920, March. Palm Springs of San Jacinto, with M. T. Barron and Fred Reed. April, two days. Palm Springs and foothills of Mount San Jacinto, looking for a rare fern; accompanied by H. M. and Carlotta Hall, who were the hosts on this trip.

BIBLIOGRAPHY OF THE WRITINGS OF SAMUEL BONSALL PARISH

1881. Plants of Southern California collected in the counties of San Bernardino, San Diego and Los Angeles. 8 pp. Oquawka, Ill.

1882. Supplementary list of plants collected in the counties of San Bernardino, San Diego and Los Angeles. 4 pp. Oquawka, Ill.

1888. Phacelia heterosperma. Bot. Gaz., 13:37–38.

1890. California Palms. Gard. and For., 3:51–52.
The botany of Slover mountain. Bot. Gaz., 15:51–53.
The palms of the Southern California border. Gard. and For., 3:542.
Notes on the naturalized plants of Southern California. I, Zoe, 1:7–10; II, *ibid.*, 1:56–59; III, *ibid.*, 1:122–126; IV, *ibid.*, 1:182–188; V, *ibid.*, 1:205–210; VI, *ibid.*, 1:261–265; VII, *ibid.*, 1:300–303.

1891. Notes on the naturalized plants of Southern California. VIII. Zoe, 2: 26–34.
The arborescent Yuccas of California. Gard. and For., 4:135–136.
Notes on California plants. I. Zoe, 2:116–117.

1892. Notes on California plants. II, III. Zoe, 2:320–322.
New California plants. Bull. Torr. Bot. Club, 19:91–93.

1893. Notes on California plants. IV. Zoe, 3:352–354.
A new Collinsia. Zoe, 4:147.
Additions to the flora of Southern California. Zoe, 4:160–167.
Morphological notes. Erythea, 1:45–47.
New station for Notholaena tenera. Erythea, 1:153–154.

1894. Distribution of the Southern California trees. Zoe, 4:332–353.

1895. Further additions to the flora of Southern California. Erythea, 3:58–62.

1896. Biographical sketch of M. S. Bebb. Erythea, 4:29–31.

1898. New or little-known plants of Southern California. I. Erythea, 6:85–92.

1899. New or little-known plants of Southern California. II. Erythea, 7:89–97.

1900. The growing periods of the Southern California ferns. Fern Bull., 8: 26–29.
Southern California forms of Phacelia circinnata Jacq. Zoe, 5:9–11.
Contributions to Southern California botany. I. Zoe, 5:71–76.

1901. Errors in the reported stations of some Southern California plants. Zoe, 5:109–120.
Southern extension of the range of Polypodium scouleri. Fern Bull., 9:40–42.
California fern gossip. Fern Bull., 9:73–77.
The flora of Snow Cañon, California. Plant World, 4:227–229.
A group of western American Solanums. Proc. Calif. Acad. Sci., ser. 3, 2:159–172.
The vegetation of Plymouth three hundred years ago. Rhodora, 3:17.

1902. Aster greatai. Bull. S. Calif. Acad. Sci., 1:15, fig. 2.
A new California rose. Bull. S. Calif. Acad. Sci., 1:87, t. 7.
Southern California species of Calochortus. I. Bull. S. Calif. Acad. Sci., 1:101–106, t. 8; II. *Ibid.*, 1:120–125.
Through desert and mountain in Southern California. Plant World, 5:121–128.
San Jacinto Mountain. Plant World, 5:236–237.
Notes on two parasitic plants. Torreya, 2:105–106.

1903. Two new plants from Southern California. Bull. S. Calif. Acad. Sci., 2: 26–28, t. 1.
A few new or rare plants from Southern California. Bull. S. Calif. Acad. Sci., 2:81–83, t. 2.
Concerning certain trees. Bull. S. Calif. Acad. Sci., 2:155–156.
A sketch of the flora of Southern California. Bot. Gaz., 36:203–222; 259–279.
Vital persistency of Agava americana. Torreya, 3:33–35, fig.

1904. A preliminary synopsis of the Southern California Cyperaceae. I, Bull. S. Calif. Acad. Sci., 3:35–37; II, *ibid.*, 3:49–56, t. 2–4; III, *ibid.*, 3:65–68, t. 5; IV, *ibid.*, 3:81–86, t. 6–8; V, *ibid.*, 3:141–143.
New or unreported plants from Southern California. Bot. Gaz., 38:459–462.
Fern flora of California. Fern Bull., 12:1–15.

1905. A preliminary synopsis of the Southern California Cyperaceae. VI, Bull. S, Calif. Acad. Sci., 4:8–13, t. 9–10; VII, *ibid.*, 4:51–52; VIII, *ibid.*, 4:66–68; IX, *ibid.*, 4:80–84, t. 11–12; X, *ibid.*, 4:106–116, t. 13–18.
Cereus giganteus in California. Bull. S. Calif. Acad. Sci., 4:122.
Flowering of Yucca australis. Torreya, 5:104–105, fig.

1906. Memorial of Stephen Grout. Bull. S. Calif. Acad. Sci., 5:18–19.
A preliminary synopsis of the Southern California Cyperaceae. XI, Bull. S. Calif. Acad. Sci., 5:20–28, t. 20–21; XII, *ibid.*, 5:47–54, t. 22–23.
Teratological notes. Torreya, 6:32–34.
Botanical nomenclature at the Vienna congress. Bull. S. Calif. Acad. Sci., 5:19–20.

1907. An abnormal leaf in Rumex. Torreya, 7:184–185, fig.
Some plants erroneously or questionably attributed to Southern California. Muhlenbergia, 3:1–7.
Recent additions to the flora of Southern California. Muhlenbergia, 3: 57–62.
Notes on the flora of Palm Springs. Muhlenbergia, 3:121–128.
A contribution toward a knowledge of the genus Washingtonia. Bot. Gaz., 44:408–434, figs. 1–12.

1908. Review. Hall, Compositae of Southern California. Muhlenbergia, 4:26.
A problem in plant distribution. Muhlenbergia, 4:42–43.
Fremont in Southern California. Muhlenbergia, 4:57–62.
The flowers of Washingtonia. Bot. Gaz., 46:144–147, figs. 1–5.
Other teratological notes. Torreya, 8:164–167, fig.

1909. Additions to the Southern California flora. Bull. S. Calif. Acad. Sci., 8:7.
A bibliography of the Southern California flora. I, Bull. S. Calif. Acad. Sci., 8:71–75.
Parry and Southern California botany. Plant World, 12:158–162.

Notes on some introduced plants of Southern California. I, Muhlenbergia, 5:109–115; II, *ibid.*, 5:121–128.
Roezl and the type of Washingtonia. Bot. Gaz., 48:462–463.
Teratological forms of citrus fruits. Torreya, 9:227–229, fig.

1910. A bibliography of the Southern California flora. II, Bull. S. Calif. Acad. Sci., 9:57–62.
A Wisconsin riddle. Torreya, 10:39.
The origin of the coco palm. Torreya, 10:269–271.
Review. Spalding, Distribution and Movements of Desert Plants. Muhlenbergia, 6:4–5.
What is a subspecies? Muhlenbergia, 6:32–33.
Review. Greene, Landmarks of Botanical History. Muhlenbergia, 6:53–58.
The Southern California Juncaceae. Muhlenbergia, 6:113–120; 121–128, t. 5.
Review. Jepson, A new flora of California. Plant World, 13:14–15.
Mutation in the Oenotheras. Plant World, 13:66–68.
Review. Two New Zealand botanical reports. Plant World, 13:140–144.
Effect of cement dust on citrus trees. Plant World, 13:288–291.

1911. Additions and emendations. Muhlenbergia, 7:73–82, fig.
The earliest notes on the natural history of California. Bull. S. Calif.. Acad. Sci., 10:64–65.
Review. Chase, Conebearing Trees. Abram, Phytogeographic and Taxonomic Survey of Southern California Trees and Shrubs. Jepson, Flora of Western Middle California. Muhlenbergia, 7:55–57.

1912. Additions to the flora of Southern California. Muhlenbergia, 8:79–82.
Photographing red snow. Plant World, 15:71.
Red snow. Am. Botanist, 18:33–35.

1913. Coreopsis gigantea Hall. Muhlenbergia, 8:133–134, fig. 27.
Additions to the known flora of Southern California. Muhlenbergia, 9: 57–59.
A catalogue of plants collected in the Salton Sink (Advance separate from "The Salton Sea"). Carnegie Publ. 193:1–11, 2 maps.
Plants introduced into a desert valley as a result of irrigation. Plant World, 16:275–280.
The California Paroselas. Bot. Gaz., 55:300–313.

1914. The Tecate cypress. Bull. S. Calif. Acad. Sci., 13:11–13, t. 9. Reprinted in Calif. Cultivator.
Circulating pests. Calif. Cultivator, 42:343.
Sketches of the Colorado desert. Plant World, 17:122–130.
Plant ecology and floristics of Salton Sink ("The Skeleton Sea"). Carnegie Publ. 193:85–114.

1915. The Whitewater sands. Muhlenbergia, 9:133–139, t. 11–13.
Notes on some Southern California plants. Bull. S. Calif. Acad. Sci., 14:12–16.
Teratology of the navel orange. Bull. S. Calif. Acad. Sci., 14:46–48.
Observations in the Colorado desert. Plant World, 18:75–88, f. 1–4.
The Southern California ferns. Am. Fern Jour., 5:97–104.

1917. The Red Hill pools. Bull. S. Calif. Acad. Sci., 16:51–52.
An enumeration of the Peteridophytes and Spermatophytes of the San Bernardino Mountains. Plant World, 20:163–178, fig. 1–3; 208–223; 245–259.

1918. Additions and corrections to the above enumeration. Plant World, 21:220–221.

Notes on some Southern California plants. Bot. Gaz., 65:334–343.

1920. The immigrant plants of Southern California. Bull. S. Calif. Acad. Sci., 19[4]:3–30.

A supplementary bibliography of the Southern California flora. Bull. S. Calif. Acad. Sci., 19:24–28.

1921. On the distribution of certain trees in California. Bull. S. Calif. Acad. Sci., 20:31–33.

A reminiscence of roses. Am. Botanist, 27:60–61.

1923. Additions to the introduced flora of California. Madroño, 1:115.

Cleomella obtusiflora. Bull. S. Calif. Acad. Sci., 22:12–14.

1925. The Cactaceae, *in* Jepson's Manual of the Flowering Plants of California, 654–660.

1926. Cereus munzii. Bull. S. Calif. Acad. Sci., 25:48.

Notes on Cactaceae. Bull. S. Calif. Acad. Sci., 25:83–84.

Review. Jepson, Manual of the Flowering Plants of California. Bull. Garden Club of Am., ser. 3, 9:57–58.

University of California,
December 30, 1930.

MACROCYSTIS AND ITS HOLDFASTS

BY

WILLIAM ALBERT SETCHELL

University of California Publications in Botany
Volume 16, No. 13, pp. 445–492, plates 33–48
Issued February 27, 1932

University of California Press
Berkeley, California

Cambridge University Press
London, England

MACROCYSTIS AND ITS HOLDFASTS

BY

WILLIAM ALBERT SETCHELL

The extraordinary range of what has been usually regarded as a single species, *Macrocystis pyrifera* (Turn.) Ag., with its discontinuities, its seeming accommodation to depths of from 0–80 (or more ?) feet of water, its extreme variation as to length of axes, shape of pneumatocysts (or vesicles) and of blades (as to length, breadth, margins, surface, soration, etc.), leads one whose experience inclines him to regard narrower types of distribution as probably the normal, to seek such lines of possible cleavage as may be consistent with chorologic and ecologic variables. Herbarium studies are not satisfactory, since only fragments can be incorporated into collections. The chief herbarium or even the museum material is wholly inadequate and consists of scraps broken off from large plants and torn to pieces, which were collected either while they were floating or after they had been washed ashore. It seldom is possible to determine from what portion of the plant the adult leaves and bladders which usualy constitute the preserved material, have come. The studies of local plants, especially as to development and seasonal change, ought to furnish a more complete picture, but these are difficult and require special financing for exploration. If such studies could be carried through in the widely different yet clearly segregated areas in which the chorology of the plant is displayed, a much more definite solution might be expected of both the problem of polymorphy and the problem of chorologic disjunction. It is hoped that the morphologic and ontogenetic fragments brought forward in these notes may contribute something toward enlightment.

The general morphology and to some extent the histology and the ontogeny of *Macrocystis* have been dealt with by numerous authors and fairly recently by Skottsberg (1907, pp. 80–133) in a truly monographic fashion. As a review of what has been done, Skottsberg's account is by far the most complete and illuminating yet published and it seems unnecessary in this brief paper to attempt to go over the same ground, except to recall certain points which concern themselves, first, with the distribution of *Macrocystis* as a genus, and second, with the nature and variety of the holdfast.

The main distribution of *Macrocystis* (see pl. 48) is circumpolar in the Southern Hemisphere from about the parallel of 60° S whence it descends to about 40° S latitude. Along the western coast of South America it extends northward from latitude 40° S until it approaches the equator, where it stops. It reappears still farther north on the western coast of North America in the vicinity of Magdalena Bay in Lower California and Mexico (neighborhood of the Tropic of Cancer), and continues on northward to the neighborhood of Sitka slightly over 57° N). Although certain older records indicate a still further extension along the Aleutian Islands and Bering Sea to the Ochotsk Sea, all recent experience indicates Sitka as the extreme limit of certainty. Ruprecht (1851) in particular does not mention it as occurring in the Ochotsk, and recent examination of the Kurile Islands has not discovered it growing there. In Bering Sea and in localities of the North American coast between Bering Sea and Sitka, it seems clearly absent, except possibly as floating specimens of extra-local origin (Saunders, 1901, p. 431; Setchell and Gardner, 1903, p. 270). As Setchell and Gardner intimate (*loc. cit.*), the northward limitation of the species on the North American coast, as well as its presence along the western coast of the United States, raises the query as to whether this *Macrocystis* may be the same as that which flourishes in such abundance around Cape Horn, the Falklands, South Georgia, Kerguelen, and other Antarctic islands, where the waters are so much colder. The same query may be made as to the *Macrocystis* of much of the western coast of South America. The waters of Bering Sea, of the Ochotsk, and of the Kuriles are probably not colder than those of Cape Horn, South Georgia, the Falklands, and those of the Antarctic islands. Hence its absence presents the question: specific identities or seasonal or other variables?

The range of temperature of surface waters of the areas of distribution of *Macrocystis* extends from 0° to 5° C (South Georgia, etc.), 5° to 10° C (Kerguelen, Fuegia, Falklands, etc.), 10° to 15° C (southern Chili, southern New Zealand, southeastern Alaska to Oregon, etc.), and 12° to 15° to 20° C (North Island of New Zealand, California, and Cape of Good Hope). From the range of temperature, some two or even three species of reasonable cleavage might be expected, but nothing of this has as yet been detected, as may be seen from Skottsberg's review of the situation. Attention is directed primarily to the consideration of this matter in the Flora Antarctica of the Botany of the British Antarctic Expedition of 1839–1843 (vol. 2, pp. 461–466,

pl. 169–171, Dec. 6, 1846), where Hooker, whose experience was most extensive, dissents from the early point of view of Bory (1826) and even of C. A. Agardh (1835) and states his very definite opinion that all forms described may be considered as belonging to one species. There is so much to be said for this point of view that one hesitates even to accept the point of view of Areschoug (1883, p. 22) and of M. A. Howe (1914, pp. 60–66, pl. 18–24) as to segregation into two species without most careful and critical scrutiny of the evidence. The cleavage of Areschoug and of M. A. Howe is based on the basal structures, as to the possession of a flattened rhizome-like structure or the absence of it. This structure was first depicted, but not described, by Postels and Ruprecht (1840, pl. 5) under the name of "*Macrocystis angustifolia* Bory," the plant pictured being from the coast of Chile. Another Chilean plant, with the holdfast more usually considered as typical (but seemingly fairly young) is also figured by Postels and Ruprecht (*loc. cit.*, pl. 6), as *Macrocystis pyrifera.* They further figure as *M. tenuifolia,* a plant from the northwestern coast of North America ("Norfolk Sound," now called Sitka Sound) which at least lacks a flattened rhizome. Areschoug (*loc. cit.*) very clearly describes the flattened rhizome of the *Macrocystis angustifolia* Bory, so far as the Chilean specimens are concerned, and emphasizes the segregation of this species from the main body of variants of the collective *M. pyrifera* (L.) Ag. Skottsberg (*loc. cit.*, pp. 112–114) discusses the rhizome relation and refers to it as a distinct form, *Macrocystis pyrifera* f. *angustifolia.* M. A. Howe, in his studies of the Peruvian algae collected by Coker (1914, pp. 60–64, pl. 18–22), describes and illustrates this plant of the western South American coast and refers it, by a process of exclusion, to *Macrocystis integrifolia* Bory. The same idea of segregation and the name chosen by Howe were used by Setchell and Gardner (1925, pp. 629, 630, pl. 62), with certain reservation as to the possible close relationship between the two plants there described as they occur on the Pacific coast of North America. It is to be suspected that within the northern limits of the range, the species (or form) represented is that provided with the flattened and repent main axis (or rhizome). This was found to be the case all along the western coast of Vancouver Island in 1930, where in June and July the only patches seen were of the *Macrocystis integrifolia* type. The known distribution of this species extends from the upper end of Vancouver Island (probably even from Sitka) to the Monterey Peninsula. No specimens have been seen from southern

or Lower California. In fact, there seems to be some reason for believing that the *Macrocystis* with the flattened rhizome is the only one occurring north of Point Conception on the western coast of North America. More extensive collecting is necessary to make certain of this, but a number of facts point strongly toward such a conclusion. J. S. Burd (1915, p. 198) finds as a result of his analyses, that the specimens from the north (Monterey Peninsula) "are distinctly superior in nitrogen, phosphoric acid, and potash, but slightly inferior in iodine content." There is a distinctly different type of *Macrocystis* vegetation south of Point Conception, in that the "groves" parallel to the shoreline occur in distinctly deeper water formations than anything of the kind found north of this Point (Cameron and associates, 1912, 1914). The only plants of *Macrocystis* definitely placed, so far, north of Point Conception are of the *M. integrifolia,* and south of it, the *M. pyrifera* type.

There is at Moss Beach, San Mateo County, California, a colony of the rhizome-possessing *Macrocystis* (or *M. integrifolia* Bory) and scattered observations have been made upon it. It is attached to clumps of mussels growing on the rocks in narrow clefts where the waves form currents at times of low water. The attachments are just above and just below the lowest tide marks. The fronds are several meters long; the leaves are rather narrow, varying from entire through slightly toothed to those regularly spinulose-dentate, the teeth being slender, narrowly cylindric-conical, and up to 7 or 8 mm. long. The leaf surfaces are smooth to longitudinally wrinkled and the vesicles vary from almost globular to elongate pyriform. On a single plant there may at times be found all variations between the leaf types of *Macrocystis angustifolia* and *M. integrifolia* as illustrated by Bory (1826, pl. 6 and 8). Some are even of the leaf type of *M. pomifera* Bory (*loc. cit.,* p. 9).

The rhizomes are similar to, but more robust than those of the Peruvian specimen of *Macrocystis integrifolia* illustrated by M. A. Howe (1914, pl. 20) and in the specimens distributed by him (No. 09600). They are well illustrated by Setchell and Gardner (1925, pl. 62). There is a possibility that the plant of Pacific North America differs from that of Pacific South America, but it seems best to regard them as within the same specific group, at least, for the present.

The locality at Moss Beach, being fairly accessible, has been visited from time to time during many years. The plants seem to persist in the same limited locality and while there is some difference in size,

there is little evidence that new plants are appearing. In early January, 1925, however, H. E. Parks and the writer discovered several young plants, ranging from one which had five leaves but without prostrate, flattened, or rooting stem, to one which showed numerous leaves and the lower joints of the stem flattening, becoming prostrate, and sending off marginal hapteres. Three of these young plants have been either photographed or drawn and are shown in plates 33, 34, and 35. The earliest stage found (pl. 33) cannot be distinguished from that of the plant called *Macrocystis pyrifera*, the deeper-water plant of southern California. The holdfast is symmetrical and does not show any inclination to become decumbent or horizontal. Its primary or basal joint (or segment) is cylindrical and erect, smooth (i. e., without incipient hapteres), and forking at the tip into two joints, equal, diverging, each bearing toward the inside an undivided blade or leaf with unswollen stalk, and with margins mostly entire but with two or three widely spaced spinulose teeth while the outer side of each second joint bears a short branch with terminal scimitar-shaped blade, dividing unilaterally to produce a row of blades. Each of the blades produced on this branch have basal vesicles (either formed or forming), indicating that this is a true branch of the final order, that is, one which has ceased to have the possibility of further dichotomy (whether equal or unequal). In all of the five young plants found, this first outer branch becomes differentiated at once into the strictly unilateral type with all the blades provided with vesicles. There are of probable occurrence, however, young plants in which these first outer branches have one or more of the lower blades without bladders and, therefore, capable of dichotomous division, although unequally. These may produce, in turn, other branches and, instead of a simple, unilateral branch, produce two or three unilateral branches. This is commonly the case in *Macrocystis* of both types in the divisions after the first unequal dichotomy and gives rise to the multiple pseudo-dichotomous branching of the basal portions of older plants. This will be considered in the succeeding paragraphs. The desire here is to emphasize the essential differences between the first branching, which is equally or truly dichotomous, the second and other intermediate branchings, which are unequally or pseudo-dichotomous, and the long simple branches ultimately produced and continued in growth lengthwise from a terminal blade by unilateral splitting. Through the variance in the products of splitting of the (at the time) terminal blade, the distinctive branching of the species of *Macrocystis* (and to a less

degree that of *Pelagophycus* as well) is brought about. The splitting of the original or primitive blade is equal. The two resulting secondary blades are unequal, both in shape and in the results of their splitting. The two products of the splitting of each may differentiate, the one into a blade which splits slightly unequally or almost equally, or into one which is largely but not extremely unequal, or into one whose splitting becomes absolutely unilateral, the products becoming blades provided with bladders and with multiple blades of limited growth, or blades with bladders and single blades of limited growth.

A slightly more advanced stage is represented on plate 34. This plant has started to become decumbent at the very base, the holdfast is spread out dorsiventrally. The first joint is becoming flattened (or at least compressed) and is producing hapteres along two sides. The first dichotomy (*A*) is equal and is producing a single lateral haptere on one of the forks. The outer lateral branches (*B, B*) are simple with all the blades provided with vesicles and the lower blades are showing a tendency to split above the vesicles. The inner branches are developing and showing the unequal splitting, the outer blades (*D, D, D*) without incipient vesicles and tending to split again, while the inner blades (*C, C*) are showing the incipient vesicles indicating the beginnings of unilateral (unbranched) branches. This plant shows the tendency of young *Macrocystis* plants to alternate the two types of branches; the two first unilaterals being outer, the two second unilaterals being inner, with reference to the middle of the angle of the first dichotomy.

Plate 35 shows a plant slightly further developed than the one represented in plate 34. The letters refer to the same parts as are indicated on plate 34. The holdfast is much the same but the incipient hapteres have increased in number on the edges of both arms of the first dichotomy; the two outer branches (*B, B*) have developed further and show clearly the ultimate type of unilateral branching whose blades are all provided with vesicles. The second pair (*C, C*) of ultimate unilateral branches show clearly both their nature and their relation to the further development of the unequally dividing inner portion of the blade from which both *C* and *D* have sprung. Each is dividing further and probably in a less unequal fashion. The further progress seems fairly clear; the flattening main branches become more and more decumbent, give off more and more hapteres from their edges, the new stems (as distinguished from the differentiated unilateral branches) increase in number, and the clump of rhizomes and hapteres with its trailing, long simple branches with bladder-bearing

leaves develops. The bladders, at first approaching a globular shape, passing into a broadly, then more narrowly pyriform shape, finally become elongated to from three to four times (at least) as long as they are broad (narrowly elongate-pyriform). The blades of the leaves vary from almost entire to abundantly spinulose-serrate, from narrow to fairly broad, and from smooth to delicately or deeply longitudinally rugose. The holdfasts, in the specimens attached near low-water mark are usually about 15–20 cm. across and low conical, but large, heavy holdfasts are cast ashore from deeper water (pl. 36), which are much higher as well as broader and surmounted by a mass of flattened bases of erect or partially decumbent stems. Such a holdfast, somewhat battered, is represented on plate 36. Its horizontal diameter was about 36 cm. when fresh and its height very nearly as great. This holdfast came ashore at Pacific Grove, not far from Point Pinos, in Monterey County, California, and was by no means the largest one observed. When dissected, it showed many layers (oblique) of flattened rhizomes clambering over one another, one layer of which is represented on plate 37. Much more investigation of this deeper-water plant is necessary, but the evidence thus far suggests, but does not prove, that the *Macrocystis* occurring north of Point Conception, California, even to Sitka, Alaska, may be entirely made up of the flattened rhizome-producing species (*M. integrifolia* Bory). Likewise, no occurrence of the rhizome-producing *Macrocystis* has as yet been made known from the coast of North America to the south of Point Conception.

Postels and Ruprecht (1840, pl. 5) were the first to figure what seemed at least to be a *Macrocystis* with a flattened rhizome, although the flattened quality, while plausible, is not absolutely certain. Skottsberg (1907, p. 112) has alluded to this figure and Areschoug (1883, p. 22) has described a Chilean plant, regarded as *Macrocystis angustifolia* Bory (which it probably is, at least *pro parte*), with a flattened rhizome, both of whose margins emit roots and very long cauliform trunks. Areschoug's specimens, preserved in the herbarium of the Royal Swedish Academy at Stockholm, show the broad, flattened rhizome very well. Skottsberg (1907, p. 113, fig. 132) gives a figure of such a rhizome, but the specimen must have been very imperfect, since it is not at all characteristic. The Peruvian *Macrocystis,* described and figured by M. A. Howe (1914, pp. 60–64, pl. 18–22) shows rhizomes answering to Areschoug's description. The central and northern California specimens, as well as those from Washington

and British Columbia, have flattened rhizomes, very similar to if not identical in form, etc., with those of the Chilean and Peruvian plants. The figure of Setchell and Gardner (1925, pl. 62) illustrates the general appearance of the central California plant very well. The broad flattened rhizome, closely applied to the mass of hapteres, over which and amidst which it creeps, gives off from both edges (only) regular series of hapteres and, at seemingly regular intervals, horizontal branches. The branches regularly alternate with one another and each branch gives off, on its lower edge (i.e., away from the tip of the rhizome or its branch) an erect (or free) cylindrical, unilateral branch and continues on as a flattened, repent structure to branch again and again. This may be seen, to a slight degree at any rate, in the fragment of the holdfast represented. On plate 37 is represented a portion (or layer) from the holdfast figured on plate 36. Here may be seen something of the same structures, particularly of the flattened rhizomes, indicated above.

On plate 38 are drawings of fragments of holdfasts dissected out from plants collected at Moss Beach in January, 1925. Figure 1 shows a main branch, the flattened rhizome with seemingly alternate branches of the next order (*A*, *B*, and *C*) emitted laterally and with the lateral rows of hapteres. Of these branches, *A* is soon cylindrical with branchlet *a*, seemingly at least bilaterally and fairly equally divided and without a vesicle at its base. Such a branchlet may act as a branchlet of indefinite growth and branch still further, becoming ultimately, however, more and more unequal in its dichotomy. From such branchlets the extension of the pseudo-lessonioid portion of the frond becomes possible, producing alternate branches (or branchlets) capable of still further division, as well as certain laterals which branch only unilaterally, all of whose uniseriate lateral outgrowths become vesicle-bearing leaves. At *b* is represented a branchlet with a vesicle, bearing a dichotomous blade which by even further division produced the pseudo-lessonioid bunches of leaflets, but apparently never prolonged into either pseudo-lessonioid or unilateral branches. The splitting of such a branch as *A*, from *b* on, will be unilateral and with uniseriate lateral multifoliate or unifoliate vesiculiferous outgrowths.

Branch *B* (of figure 1) is similar to branch *A*, but borne on the opposite side of the rhizome. Its left-hand division (*e*) is already of the cylindrical type, with *f* (showing a small sorus) dividing (equally?) and without any indication of vesicle production; with *g*, also evesiculiferous, dividing (seemingly unequally); with *h*, vesiculiferous and about to produce multiple blades; and the right hand

product (*i*) of the unequal division, producing a flattened continuation of the rhizome and with further divisions, of which the left hand division (*c*) promises a cylindrical branch and the right hand (*d*) a continuation of the flattened rhizome. Each segment of the horizontal rooting rhizome, that is, each portion between two flattened branches, bears normally at least, one erect, cylindrical, mostly bladder-bearing stem, but the lowest one or two segments, non-vesicle producing, may again branch, in a pseudo-lessonioid fashion and increase the number of erect branches. Figure 2 shows a similar relation of splitting of various inequalities, *D, F, G,* and *J* representing the cylindrical, erect branches and *E, L, K, H,* and *M* representing the flattened, prostrate rhizome branches (or their positions). Figure 3 shows the shape although not the extreme length of the vesicle of one of the upper leaves.

To summarize some of the important happenings in connection with the *Macrocystis* possessing flattened rhizomes, or *M. integrifolia* Bory (as understood at present), it may be recalled: (1) that the first division of the plant, already possessing a symmetrical holdfast of dichotomously branched hapteres, is equal or isotomic—practically, the only important division in the plant that is isotomic; (2) that the next complexity arises through two symmetrically placed anisotomic (or unequal) divisions through which each of the two blades derived from the isotomic division is separated into an outer cylindrical, erect branch whose further complexity arises by unilateral (or heterosotomic) fission and all (at least normally) of whose lateral members are not only secund on the stem but also developing bladders, and an inner branch, which follows the example of the primary or stipe segment and each of the two segments of the isotomic division in becoming flattened, prostrate, and emitting dichotomous hapteres along their borders; (3) that each of these rhizome products of the first anisotomic division divide again isotomically, producing (*a*) an inner erect and cylindrical (heterosotomic) branch and (*b*) an outer flattened, decumbent, haptere-producing branch which repeats in turn, in its anisotomic splitting, branches of similar heterosotomic and anisotomic characters to those of the previous splitting; (4) that this continues during the active life and growth of the plant until in the deeper portions of its habitat, large holdfasts, with many rhizome branches and many erect branches are produced; and (5) that, after the first one or two erect, cylindrical heterosotomic branches devoid of hapteres are produced, these may develop, toward the base of each, blades devoid of vesicles, which may split in an anisotomic fashion to produce, at

the first, or at least after a few divisions, erect, cylindrical, heterosotomic branches with their unilaterally arranged, vesicle-bearing leaves; (6) that after the massive, but finally crowded holdfast develops, the flattened stems may cease or delay in producing hapteres from their borders, so that the lower branches, more alternate than dichotomous, may ascend and, for a time at least, be free from one another for a considerable height (see plates 36 and 37); (7) that certain of the blades without vesicles, produced toward the bases of the erect branches, may divide in a fashion which seems definitely isotomic, producing a short cluster of dichotomies, which possibly, under certain conditions, proceed to elongate and branch in turn; and (8) that certain of the blades with vesicles, situated on the lower parts of the erect cylindrical stems, may divide exactly, or very nearly, isotomically, producing a cluster of blades at the tips of the vesicles. The divisions arising as described under 7 may, it seems probable, take part in increasing the complexity of the frond, although proof is lacking, but the divisions of the vesicle-bearing blades, described under 8, cannot be supposed to go further, since as Skottsberg (1907, p. 91) has indicated, there seems to be no evidence that a blade (or branchlet) which has developed (or started to develop) a vesicle ever proceeds to a longer-branch production.

Turning from the *Macrocystis* with the flattened repent stems, or rhizomes, which extend from about extreme low water mark down into water of usually much less than twenty meters (cf. McFarland, *in* Cameron *et al.*, 1912, particularly maps of sheets IV to VIII) and from Point Conception northward, to the southern kelps extending in their off-shore formations from Point Conception southward and growing usually in about twenty meters of water, while it seems best to cite this as *Macrocystis pyrifera* (L.) Ag., this is done with mental reservations. The Koenig specimens, with notes, on which Linnaeus (1771, p. 311) founded the species were of great length and were found "swimming" in the form of great islands in the "*Mare Æthiopicum.*" Their source may be surmised as having been somewhere among the Antarctic islands (Kerguelen, Crozets, etc.), hence flourishing at a much lower temperature range (5°–10° C seasonal range) than that of the southern coast of California (about 12°–20° C seasonal range), but, as yet, there seems to be no character on which to base attempts at separation.

The early stages up to and immediately succeeding the first (isotomic) division resemble those of the *Macrocystis integrifolia* type, described above. A series of photographs of young plants is given

by Setchell and Gardner (1925, pl. 64, 65) from California specimens. Skottsberg (1907, fig. 91–98) has given drawings of a series of young plants from the western coast of South America and also (*loc. cit.*, fig. 104, 109) a series of very young holdfasts. Skottsberg (*loc. cit.*, fig. 100, 101) has presented diagrams of the earlier divisions of the frond and a drawing of a plant whose unilateral type of long branches has reached the surface of the water. The older diagram of Hooker (1847, pl. 171 B) seems clearly faulty; at least it does not apply to the plants of either North or South America. The leafless ascending stem is out of all proportion to anything in the more recent experience of *Macrocystis.*

The series of young plants figured by Setchell and Gardner (1925, pl. 64, 65) shows the different divisions of the developing blades and stems very clearly. The youngest plants resemble *Laminaria* most closely. There is a distinct stipe and developing hapteres at the lower end. The blade splits at first equally (isotomic). Before this first split has entirely separated the two halves of the first blade, each shows basally an oblique second splitting, which is certainly unequal (anisotomic). By the time the two blades resulting from the first blade have nearly or quite separated, one or both show a second or even a third split, also anisotomic. These stages are shown on plate 64, Setchell and Gardner, 1925. The young plant shown by Setchell and Gardner on plate 65, *op. cit.*, shows the holdfast restricted to the lower portion of the stipe, the first splitting, a true dichotomy (isotomic), the two outer branches, results of an unequal dichotomy (anisotomic), whose outer branch is the result of unilateral (heterosotomic) splitting and whose blades are provided with basal vesicles, except the lowest on each branch. Those being without vesicles are presumably capable of further division and this division may be of one of two kinds: equal (isotomic), giving rise to small pseudolessonioid clusters of blades without vesicles, or possibly inaugurating unequal (anisotomic) division which may increase the number of long branches of the two kinds, limited (with heterosotomic division) or continuing unequal (or anisotomic) division, from which are derived such holdfasts and lower portions of large plants as are described in the following paragraphs.

Professor J. S. Burd and Mr. Guy R. Stewart made studies of the California kelps from the point of view of their economic value (see Burd, 1913), the field work being in charge of Mr. Stewart from whom a series of holdfasts and lower portions of the stems were obtained. This series was collected from the Point Loma beds off

San Diego, California, in August and September, 1913, and immediately carefully air-dried. After being soaked for several hours in fresh water, these holdfasts and adjacent parts recovered their original form in excellent fashion. Photographs of these present an excellent series, from very small to medium or somewhat above medium size. They are represented on plates 39 to 47, as photographed immediately after soaking out, when their appearance was practically the same as when freshly gathered.

Plates 39 and 40 represent the smallest of the four holdfasts to be discussed. Plate 39 shows one view with the hapteres intact, while plate 40 shows the opposite side with the hapteres removed to show more clearly the first forking (isotomic) with the enlarged stipe, whose extreme base, with the original group of hapteres of the young plant, has decayed and the remnants lost when the plant was pulled away from its attachment in some 15 to 30 meters of water. The stipe (the portion below the dichotomy or isotomy) is erect or nearly so, has increased in length and thickness, is obconic, and has produced numerous stout, dichotomous hapteres which are multifarious (not bifarious or distichous as in *Macrocystis integrifolia*). The arms (or segments) of the dichotomy are erect, rounded, and have produced multifarious hapteres towards their bases on the surfaces away from the inner angle of forking. Each arm of the dichotomy has produced a single simple branch (*A, A*) as a result of the strongly unequal splitting following the dichotomy. Above each single arm, the further branching is a pseudo-dichotomy resulting, through the unequal divisions (anisotomy) so that the branching appears alternate. All these branches are erect, practically cylindrical, and as yet, devoid of hapteres. *B, C, D, E, F,* and *G* indicate the main branches, each of which is again branched from two to four times in the seemingly alternate fashion, to end in seeming simple, long branches (such as *H* and *I*) which probably proceeded to rise to, or at least toward the surface. This specimen had something like thirty such branches, whose lowest leaves, probably without vesicles, may have still been capable of branching towards their bases.

Plates 41 and 42 show two views of the same side of the basal portion of a plant, plate 41 uninjured, while in plate 42 the same view is represented after removal of certain of the hapteres which obscured the stipe and dichotomy. This plant is only slightly advanced over that represented on plates 39 and 40. The stipe has lost more of its lower portion. The branching has proceeded slightly

farther and the hapteres are produced even from the upper and inner portions of the segments of the dichotomy. The two first, erect, and simple branches (*A*, *A*) are to be noted. The branches above the dichotomy are of the alternate type as in the plant previously represented.

Plates 43 and 44 show a third plant, in which the holdfast portion is more developed. Plate 43 shows the holdfast intact, while the view represented in plate 44 is from the opposite side and shows the hapteres, projecting towards the observer, clipped off to show the dichotomy. On plate 43, the two segments of the dichotomy are so covered with the multifarious hapteres as to be indicated only by the branches above them and the two first simple branches (*A*, *A*), now emerge from the region to which, and somewhat above which, haptere production has advanced. The tendency of the unequal division (or anisotomy) to produce alternately, simple, heterosotomic branches is well indicated by such branches as those labelled *L*, *L*, *M*, *N*, *N*, etc. Plate 44 shows the progress upward of haptere production. The stipe has almost worn away; the arms of the dichotomy and of one or two segments above it, while still erect and still cylindrical, are covered by the multifarious hapteres which envelop the lower portion of the plant as well as support it.

The basal portion of the largest plant of the Point Loma series is represented on plates 45 and 46. This basal portion weighed about 23.75 pounds (or about 10.770 kg.) and spread out 60 to 65 cm. in breadth. The entire weight of the plant was 88.75 pounds (or about 40.204 kg.). Such a plant must be much less developed than one whose holdfast and adjacent stems and leaves weighed 137.0 pounds (about 62.131 kg.) and whose entire weight was 435.25 pounds (about 197.378 kg.). These figures are of freshly gathered plants and are given by Burd (1916, p. 188). Unfortunately, there is no specimen available or dimensions recorded for this seemingly very large plant mentioned by Burd. It should be borne in mind that the analyses showed that the freshly gathered *Macrocystis* plant contained from about 83 per cent to about 90 per cent of moisture (see Burd, *op. cit.*, pp. 191–193). A comparison between plates 45 and 46 and plates 43 and 44 will indicate how far this largest plant of the series available for this article has proceeded in the development of its basal portions. From the broad but flattened mass of hapteres, as represented on plate 45, arise not two but about half a dozen main axes, yet, on careful scrutiny, they segregate themselves in two groups.

This is emphasized in the partial dissection represented on plate 46, where the two groups lead to the two forks of the original dichotomy. There is no longer any trace of the stipe, even on careful exploration, the two arms of what seemed, at least, to be the dichotomy were separated at the lowest point to which they could be traced. There is no longer any indication of the first two simple branches (such as are represented by *A, A,* on plates 39–44), and the number of ultimate, erect, simple branches has increased many fold. Something of this may be seen on plate 47, which shows one of the two main groups relieved of basal hapteres and spread out to show the branching. The specimen shown on plate 47, although only half of the branching system of the plant, shows not only the extent to which branching may proceed, but illustrates the appearance of *lessonioid* branching, since the first impression is that the "dichotomies" are equal (isotomic), but a closer examination will show what has already been indicated by the previous specimens, that, from the very young plant up to this one, and undoubtedly in very old or at least more developed plants, the process of unequal dichotomy continues, and we may speak of at least three or possibly four types of branching, or dissection, the first true dichotomy (isotomic), where the equal splitting is confined to the first splitting, resolving the juvenile, laminarioid plants into two equal parts, each behaving the same in its future development; second, possibly as a distinct type, the equal splitting found in blades low down on the ultimate branches, with or without vesicles and resulting, usually at least, in a short, truly dichotomous cluster of narrow blades, a branchlet, or "kurzspross" of limited growth; third, the unequal splitting which results in the mass of "lessonioid," or better, pseudo-lessonioid forkings at the base of the plant, the splitting being anisotomic, not only in appearance (which may be slight) but in the diversity of the two branches produced; and fourth, the unilateral splitting of the terminal blade of the elongated ultimate branches with their leaves, with vesicles arranged along one side of the axis. The three types of splitting, isotomic, anisotomic, and heterosotomic, with the four or even five types of products, produce the complexity of the adult frond, above the holdfast.

The branching of both species of *Macrosystis,* less evident in the *M. integrifolia* than in the *M. pyrifera* of the California coast, may be seen upon comparison of the plants figured, especially the more advanced plants of the two species, such as are represented on plates 45 and 46 and on plates 37 and 38, respectively. The general plan

seems to be the same and may be compared with the plan of branching of certain cymose or cymoid inflorescences. Beginning after the fashion of a true cyme, it is truly isotomic only at first, although later certain isotomic types of division may occur in limited number and on arrested(?) laterals, it proceeds toward the ultimate scorpioid (heterosotomic) type, passing through compound stages similar to paniculate scorpioid or helicoid inflorescences, through various degrees of unequal (anisotomic) division. There is, therefore, a general tendency from the cymose to paniculate cymose, or even paniculately falsely racemose branching, to the type of the strictly unilateral (scorpioid) raceme (or scorpioid cyme).

The holdfast is progressively developed. There seems to be a primitive disk in the youngest plants, above which hapteres emerge to form the primitive holdfast at the base of the stipe. As development proceeds, the stipe develops lateral hapteres and, as branching goes further and further, the forks of the dichotomy and even of the segments beyond also develop hapteres, which become elongated and branch dichotomously (isotomic) until some of them become very much elongated. The arrangement of the hapteres is different in the two species. In *Macrosystis pyrifera* they are multifarious on the cylindrical segments, while in *M. integrifolia* they are bifarious on the margins (or borders) of the flattened segments. Since the stipe and lower branches of the latter species become flattened and hapterose even in the juvenile stages, this difference must be regarded as characteristic and justifies the opinion that the two species are distinct entities.

The intention of this paper has been to illustrate and, by brief description and discussion, to make clear the basal growth, that is, of holdfast and branching of the axes, of *Macrocystis,* as well as to examine into the status of at least the two seeming distinct species of the Pacific coast of North America. It hopes to supplement and clarify the statements of various authors, from Linnaeus (1771) to Skottsberg (1907), M. A. Howe (1914), and Setchell and Gardner (1925). The previous discussions have concerned chiefly either the division of juvenile fronds or the method of development of the erect (and largely unbranched) branches which rise to or toward the surface. While many smaller points still await further study, it is hoped that the holdfast development and the ramifications connected with it or immediately above it, have made this situation clearer than it was before this article was written.

LIST OF WORKS CONSULTED

Agardh, C.

1820. Species Algarum, 1, pt. 1.

1839 (1835?). Revision der Algengattung Macrocystis. Acad. Caes. Leop., Nova Acta, 19:281–317 (read 1835).

Agardh, J. G.

1848. Species, Genera, et Ordines Algarum, I.

Areschoug, J. E.

1883. Observationes Phycologicae, part. quarta.

Bory de Saint-Vincent

1826. Macrocyste. *Macrocystis* Bot. Crypt. (Hydrophytes). Dict. Class. d'hist. nat., 10:8–10.

1826*a*. *In* Duperry, Voy. aut du Monde—Coquille. Atlas.

1827. Cryptogamie, *in* Duperrey, Voy. aut. du Monde—Coquille, 2, 1:83–97 (for dates of issue, see Jour. Bot., 39:206).

Burd, John S.

1915. The economic value of the coast kelps. Univ. Calif. Publ., Coll. of Agr., Agr. Expt. Sta., Bull. No. 248.

Cameron, Frank K. (with assistance of others)

1912. A preliminary report on the fertilizer resources of the United States. Senate Document, No. 190, 62nd Cong., 2nd session.

Cotton, A. D.

1915. Cryptogams from the Falkland Islands collected by Mrs. Vallentin and described by A. D. Cotton, F.L.S., Jour. Linn. Soc., 43:167–168.

Goebel, Dr. K.

1891. Pflanzenbiologische Schilderungen. Zweiter teil, 321–325.

Harvey, William Henry

1862. Phycologia australica, 4:(pl. 202).

Hoffmann, Edna Juanita

1911. Fructification of Macrocystis. Univ. Calif. Publ. Bot., 4:151–158, pl. 20.

Hooker, Joseph Dalton

1845–1847. The botany of the Antarctic voyage of H.M. Discovery Ships Erebus and Terror. Flora Antarctica, part 2 (1846 is date of pages quoted).

Howe, Marshall Avery

1914. The marine algae of Peru. Mem. Torrey Bot. Club, 15.

Humboldt, F. H. N. von, et Amatus Bonpland

Plantae aequinoctiales. (Not seen.)

Janczewski, Ed. de

1875. Observations sur l'accroissement du thalle des Phéosporées. Mem. Soc. Nat. Sci. Nat. Cherbourg, 19:112–113.

Kjellmann, F. R.
1893. Laminariaceae, *in* Engler und Prantl, Die natürl. Pfl.-fam., 1 Th., 2 Abt., Lief. 97, pp. 242–260.

Linnaeus, Carolus
1771. Mantissa plantarum altera et specierum editionis II.

MacMillan, Conway
1902. The kelps of Juan de Fuca. Postelsia, 1901, p. 218.

Montagne, C.
1839. Sertum Patagonicum (*in* Alcide D'Orbigny, Voy. dans l'Amer. Merid.). (Not seen.)

Postels, A., et F. Ruprecht
1840. Illustrationes Algarum.

Reinke, J.
1903. Studien zur vergleichenden Entwickelungsgeschichte der Laminariaceae. (Kiel.)

Reinsch, P. F.
1890. Zur Meeresalgenflora von Süd Georgia. Die internat. Polarforschung. Die deut. Exp., 2:417, 418, pl. 16, f. 7*a*, 7*b*.

Rosenthal, O.
1890. Zur Kenntniss von Macrocystis und Thalassiophyllum. Flora, 73:105–147, pl. 7, 8.

Ruprecht, F. J.
1851. Tange des Ochotskischen Meeres, *in* Middendorff's sibirische Reise, 1:2, Botanik.

Saunders, De Alton
1901. The Algae. Papers from the Harriman Alaska Expedition, XXV. Proc. Wash. Acad. Sci., 3.

Setchell, William Albert
1893. On the classification and geographical distribution of the Laminariaceae. Trans. Connecticut Acad., 9:333–375.
1896. Notes on Kelps. Erythea, 4:44.

Setchell, William Albert, and Nathaniel Lyon Gardner
1903. Algae of northwestern America. Univ. Calif. Publ. Bot., 1:270.
1925. The marine algae of the Pacific coast of North America. Part III. Melanophyceae. *Ibid.*, 8:3.

Skottsberg, Carl
1907. Zur Kenntniss der subantarktischen und antarktischen Meeresalgen. I. Phaeophyceen, Wiss. Ergebn. der Schwed. Südpolar-Exp. 1901–1903, 4:6.

Turner, Dawson
1809. Fuci, 2:103, 104, pl. 110.

Will, Dr. H.
1884. Zur Anatomie von *Macrocystis luxurians*. Bot. Zeit., 42:801–808, 825–830, pl. 12.

EXPLANATION OF PLATES

PLATE 33

Macrocystis integrifolia Bory

Youngest plant thus far collected. Moss Beach, San Mateo County, California, January 8–10, 1925. Setchell and Parks. Size indicated by millimeter scale. Photographed by W. C. Matthews.



PLATE 34

Macrocystis integrifolia Bory

Slightly more advanced plant of same collection as that of plate 33, showing: holdfast and stipe already decumbent; the flattening of the lower parts of the dividing axes; the isotomy at *A*; the two first branches (*B, B*) with their terminal blades (heterosotomic); and the anisotomies giving rise to the unequal segments. *C, C,* and *D, D, D.* × ⅓ diam. Drawing by Anna Hamilton.

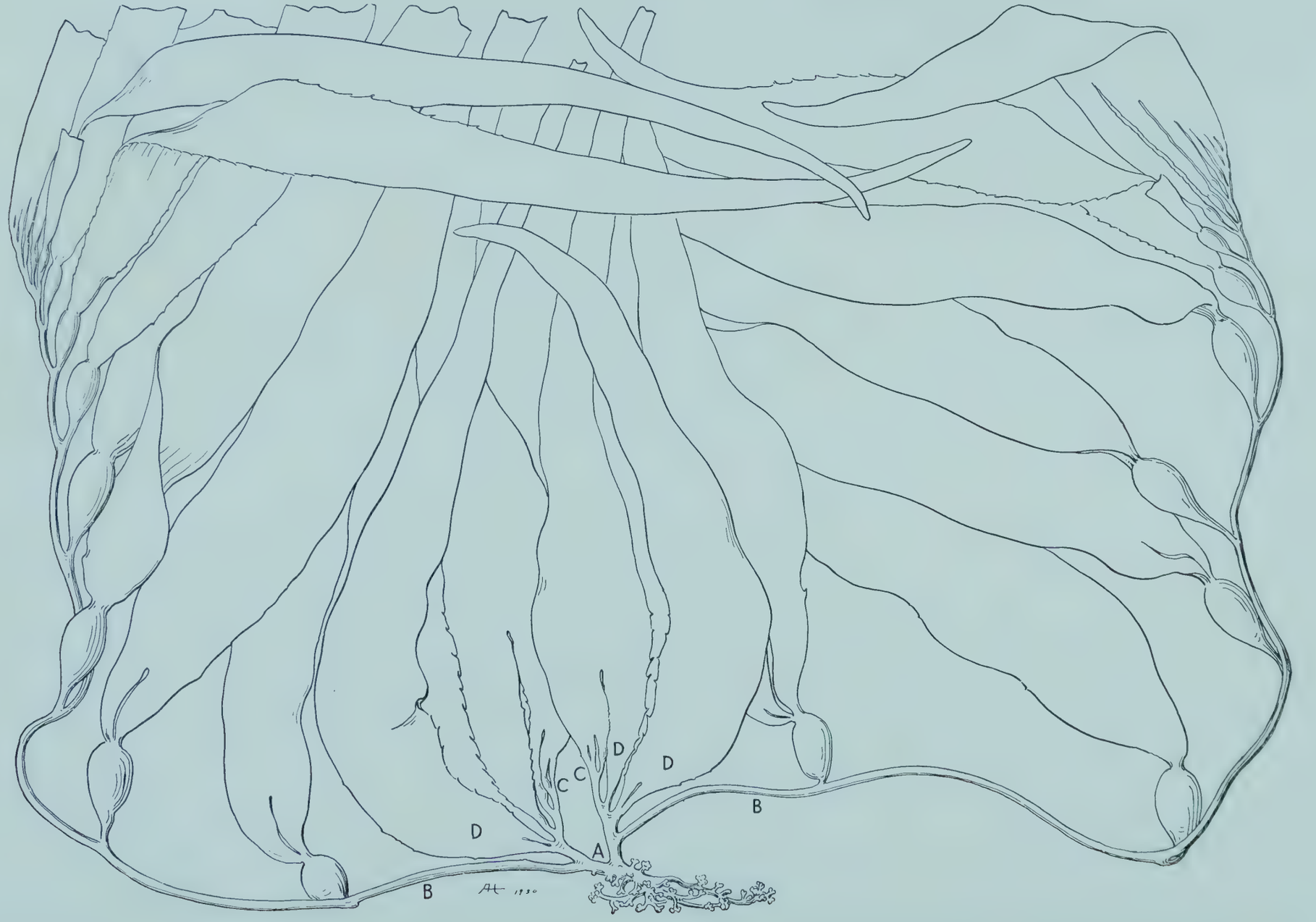

A
B
B
C
C
D
D
D
D

PLATE 35

Macrocystis integrifolia Bory

Still more advanced plant of same collection as those of plates 33 and 34, showing: advance in all features as may be seen from comparison of *A*, *B*, *C*, and D. × ⅓ diam. Drawing by Anna Hamilton.

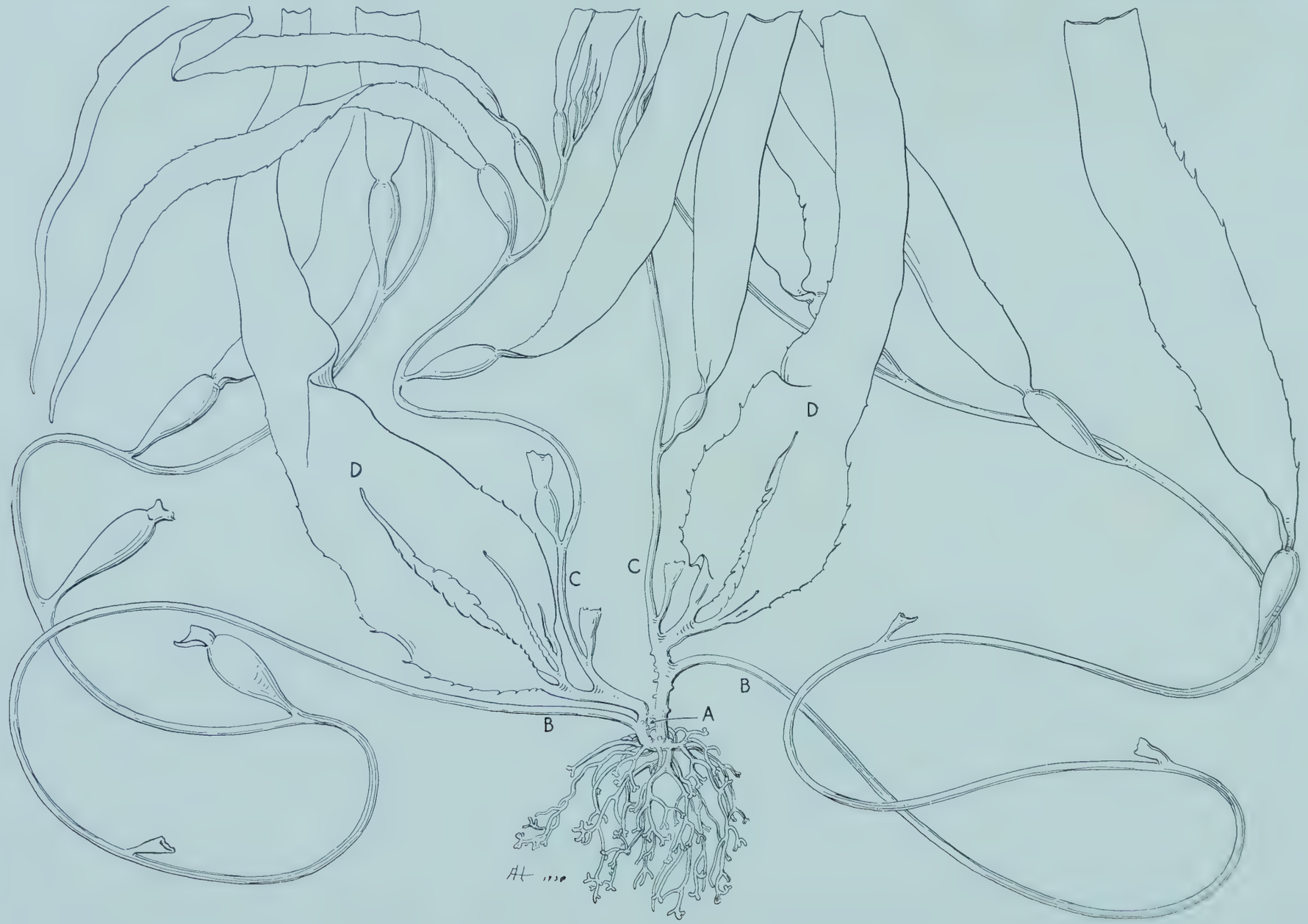

D
C
C
D
B
A
B

PLATE 36

Macrocystis integrifolia Bory

Lateral view of holdfast cast ashore at Pacific Grove, California, showing: mass of hapteres of a plant of considerable age, with the very considerable number of the upper flattened, anisotomic axes, as yet devoid of hapteres arising from it. Size indicated by millimeter scale. Photograph by W. C. Matthews.



PLATE 37

Macrocystis integrifolia Bory

A vertical section of flattened axes, removed from the upper portion of the holdfast represented on plate 36, showing anisotomic flattened branches passing into flattened rhizomes with bifarious hapteres below. Size indicated by millimeter scale. Photograph by W. C. Matthews.



PLATE 38

Macrocystis integrifolia Bory

Fragments of rhizomes from Moss Beach specimen, dissected out to show: flattening, anisotomy, and resulting branches. Explanation in the text. × ⅓ diam. Drawing by Anna Hamilton.


a
b
3
A
c
C
d
1
B
e
i
h
f
g
K
J
I
G
H
M
D
E
F
2
L
1930

PLATE 39

Macrocystis pyrifera (L.) Ag.

Holdfast and lower portions of axes of one of a series of plants (represented in plates 39–47) collected in 16–20 fathoms of water off Point Loma, California, by Guy R. Stewart, in connection with chemical work related to the economic value of kelps, by John S. Burd and himself, in August and September, 1913, showing: hapteres from the stipe (concealed) and lower portions of the arms of the isotomy; *A*, *A*, first heterosotomic branches; *B*–*I*, successive anisotomic branches. Size indicated by millimeter scale. Photograph by W. C. Matthews.


I
H
G
F
D
E
C
B
A
A

PLATE 40

Macrocystis pyrifera (L.) Ag.

Same holdfast as in plate 39, from reverse side, with certain hapteres cut away to show: stipe and fork of isotomy with bases of hapteres remaining; anisotomic branches as in plate 39 so far as visible. Size as indicated by millimeter scale. Photograph by W. C. Matthews.


G
F
D
E
B
C
A
A
3

PLATE 41

Macrocystis pyrifera (L.) Ag.

Holdfast of somewhat more advanced plant, showing: similar features to that shown on plate 39, but development of hapteres having proceeded higher up on the isotomy. Size as indicated by millimeter scale. Photograph by W. C. Matthews.


H
G
I
E
F
D
C
B
A
A

PLATE 42

Same holdfast and same view as on plate 41, but certain hapteres removed to expose lower portions, showing: stipe well eroded; arms of isotomy well covered by multifarious hapteres which reach even above the first (pair of) anisotomic branches (*A, A*), the latter being simple (and heterosotomic). Size indicated by millimeter scale. Photograph by W. C. Matthews.


H
G
E
F
D
C
B
A
A

PLATE 43

Holdfast of still more advanced plant, showing: definite advance of the haptere production (upward); the first (pair of) anisotomic branches (*A*, *A*) now with their bases concealed, and anisotomic branching (seeming alternate) above; simple (heterosotomic) type of branches indicated at *L*, *L*, *M*, *M*, and *N*. Size indicated by millimeter scale. Photograph by W. C. Matthews.


N
N
M
L
L
A
A

PLATE 44

Reverse view of same holdfast as in plate 43, with certain hapteres removed to show: complexity of haptere production (multifarious) over the arms of the isotomy and segments above it; simple branches lettered as in plate 43. Size indicated by millimeter scale. Photograph by W. C. Matthews.


N
M
L
L

PLATE 45

Macrocystis pyrifera (L.) Ag.

Largest of the holdfasts available to the writer from Stewart's collection from the Point Loma beds. The weight when freshly gathered was 23.75 pounds (about 10.770 kg.), but it was by no means the largest, or at least heaviest, basal portion collected. One weighed 137.0 pounds (about 62.131 kg.), probably due to much more extensive basal (anisotomic) division as well as greater diameter and thickness of the mass of hapteres of the holdfast proper. This view represents the uninjured holdfast and adjacent axes, showing: the basal divisions arising through the mass of hapteres in two groups, but each group consisting of several divisions. Size indicated by a stick divided into decimeters. Photograph by W. C. Matthews.


4

PLATE 46

Macrocystis pyrifera (L.) Ag.

View of lower portion of same plant as represented on plate 45, but hapteres removed over a sufficient sector to show: the two groups of axes to about the place whence they arose from the stipe, no trace of which is now present; the multifarious production of hapteres to somewhat above that represented on plate 44; and the increase in the division (anisotomic) of the axes above the upper limits of haptere production. Size indicated by the decimeters of the stick. Photograph by W. C. Matthews.


4
1
2
3
4
5
6

PLATE 47

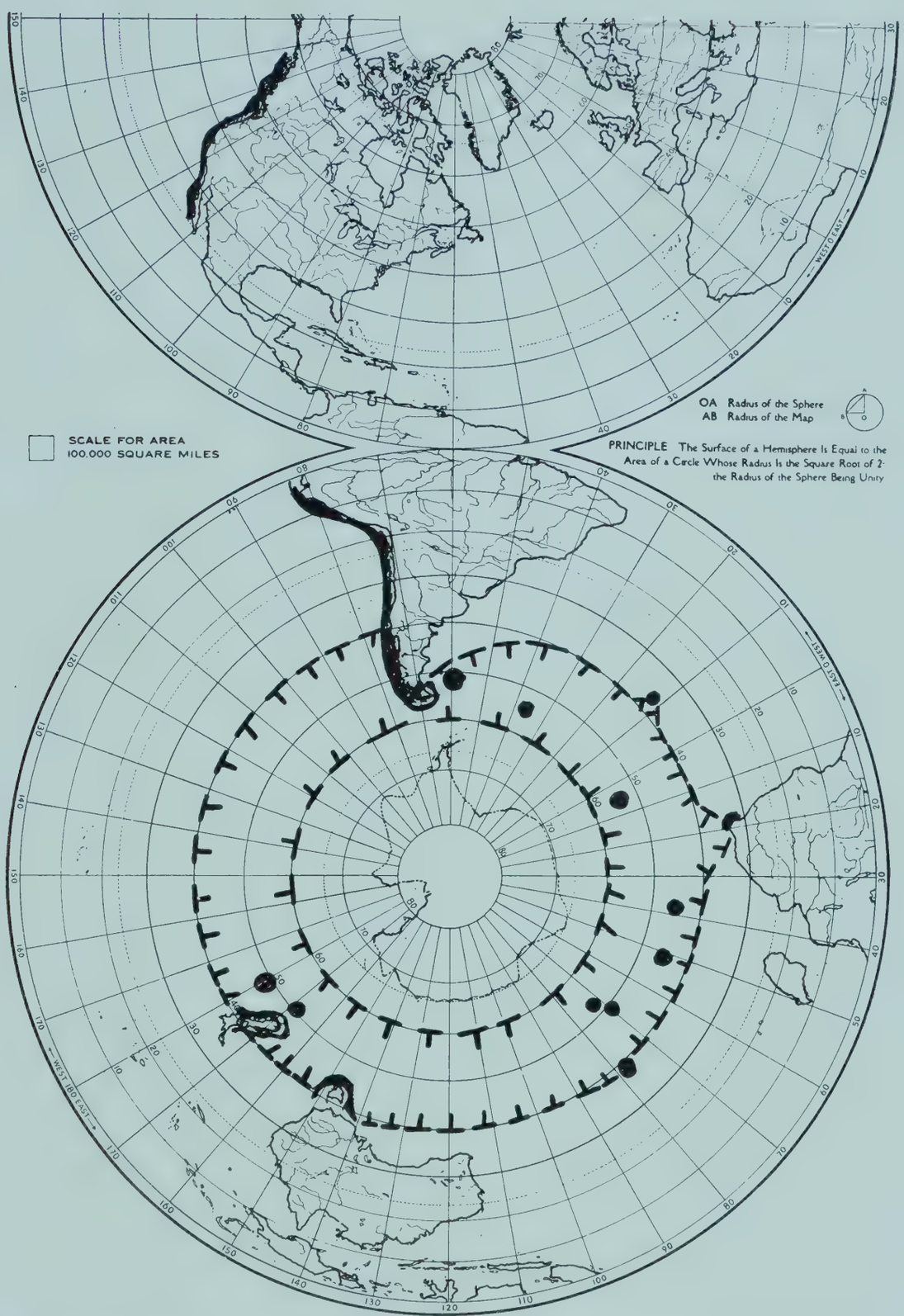
Macrocystis pyrifera (L.) Ag.

One of the two main groups of axes of the plant represented on plates 45 and 46, dissected and spread out to show: the progress of the unequal (anisotomic) division of the basal portion of the frond, giving the appearance of alternate arrangement so characteristic of the pseudo-lessonioid basal portions of the frond. Size indicated by the decimeters of the stick. Photograph by W. C. Matthews.


4

PLATE 48

Distribution of *Macrocystis*, as revised, represented on a partial map of the world in polar hemispheres, Lambert's azimuthal equal area projection. Adapted from Map No. 101P of the Goode Series of Base Maps and Graphs, by permission of the University of Chicago Press.



Adapted from Map No. 101P of the Goode Series of Base Maps and Graphs, by permission of the University of Chicago Press.

5539